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The Genus in Evolutionary Taxonomy — *A. J. Cain* — 97

Geographic Variation and the Subspecies — *N. W. Gillham* — 110

Evolution and Systematics of Ciliates (II) — *J. O. Corliss* — 121

Points of View

Problems of Family Nomenclature · *McMichael* — 141

Significance of Gaps in Pelecypod Morphology · *Nicol* — 143

Taxonomic Characters in Mollusca · *Burch* — 144

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The Genus in Evolutionary Taxonomy

A. J. CAIN

THE idea of the genus as the smallest "kind" of plant or animal that can be recognised without close study was an extremely important one in the earlier periods of taxonomy (Bartlett, 1940). The species was a subdivision of it, often requiring expert examination both before it could be recognised and before it could be named, since the specific name was at once a qualification of the generic name and a differentiation from all other specific names within that genus. Hence the custom of putting the generic name first. More than a trace of this same attitude to the genus can be seen in the results of Anderson's minor census (1940) of botanical opinion, which revealed a high proportion in favour of the view that the genus is more natural than the species. It is presumably the extreme usefulness of the genus taken in this sense that leads Just (1953) to affirm that "from a purely systematic point of view, the genus still comprises [sic] the most effective taxonomic unit on which new classifications of higher groups can be based. . . ."

Linnaeus seems to me to stand halfway between this earlier practice and more modern ones. For naming, he retains the older ideas and states emphatically (*Critica Botanica,* Hort's translation, Aphorism 257, for example) that "the Genus must be established before the [specific] name is settled, so that in each genus we may recognise the species which we are supposed to be distinguishing. For the specific name is not given us alive, unless it has a head: the head is the generic name." It is not merely fanciful, surely, to believe that such an attitude was necessary in days when the production of keys, and sound rules for name-formation, the operation of which would produce agreed synonymies, was of the first importance.

But on the other hand, his attitude to the species is much more modern. Ramsbottom (1938) has given an excellent survey of Linnaeus's opinions and Svenson (1945) has discussed much of their historical background. Svenson points out that, as soon as (and not until) the doctrine of a general and frequent transmutation of species had been brought into disrepute, the species could be regarded with confidence as a morphologically stable group of individuals, "breeding true." It then became a unit within the genus, equally susceptible of definition. The idea of its constancy, the doctrine of the immutability of species, has been of great use in the development of modern taxonomy. That Linnaeus in later years came to consider that species were not wholly immutable, as Ramsbottom has pointed out, does not mean that he returned to a chaos, comparatively speaking, of fluctuating forms within each genus. He, like his predecessors, knew far too many distinct species, apparently immutable apart from phenotypical variation. Hybrids were to be recognised as such, but if they achieved relative constancy, then they merited the status of species.

These views are well expressed in his method of nomenclature. The generic name was a single word, denoting a general kind of plant or animal. His name for a species was a phrase, not exceeding twelve words and preferably as short as possible, which was descriptive. It either referred to some striking character by which the species could be distinguished

from all others of the genus so far discovered—this was best—or gave several characters, the combination of which served to distinguish it. Such names require re-examination and amendment every time a new species is introduced into the genus. The binomial name was only supplementary to the polynomial phrase-name.

In consequence, Linnaeus found it necessary to consider species as separate entities, while naming them as parts of genera. His ideas on the nature of the genus are of special interest. Svenson quotes him as saying, in the preface to *Genera Plantarum,* "Genera . . . therefore, are as many as there are common attributes next [in rank] to those of distinct species, such as were created in the beginning: this is confirmed by revelation, experiment and observation. Hence *all genera and species are natural.*" Svenson remarks that "natural" here means that genera and species were created units, "and it was the duty of man to group together those species which belonged to a genus." He continues:

> As Spring and others have pointed out, most of our genera are not natural units; but merely represent a stage of classification above that of the species. Nor did the doctrine of descent with modifications of Lamarck and Darwin ease the Genus problem, since it introduced the additional element of time into a system which had been preeminently concerned with the nomenclature of plants and animals as they are distributed in space. To this problem of the Genus, Linnaeus seems to have given a good answer. "The limits of a genus cannot be determined until all the species of the genus are known." In the author's opinion, the attempt to make all genera "natural," without some conventional limitations, would be destructive to nomenclature, which is built up primarily on a basis of history and usage.

That Linnaeus was much interested in the production of a natural classification, based on the relationships of all parts, not on one (e.g. the fructification)is well known. Apparently, from Svenson's quotation given above and from many remarks in the *Critica Botanica,* he believed that all species could be grouped into genera between which there were definite discontinuities of attributes. The final definition of each genus as a natural group would have to wait until all the species in it were known. Presumably the genera which seemed separate only through ignorance would then be duly interconnected by newly discovered species, and exactly which attributes were merely shared by a few species and which were indeed characteristic of particular genera could then be determined.

We may well smile (and sigh) at the idea that all our problems in classification at the generic level would be over if we could discover all the separate created forms of life. On the contrary, the more that is known of a group and its past history, the more will evolutionary continuity appear and the less will enumeration of forms supposedly distinct, or actually distinct at any one period, help us. We must face up to at least four problems.

(i) Groups discrete at the present day will become indistinguishable as we pass back in time, yet we are committed to a hierarchy of discrete groups.

(ii) There is no theoretical or practical justification at all for believing that all genera are clearly discrete at any one time, since there is no law governing and *quantifying* the angles of divergence of different stocks branching from the same evolutionary line. The discovery of new species may merely confuse the situation by supplying isolated forms half-way between two genera and equally well included in both or neither, without supplying others to connect them clearly with only one.

(iii) There is no reason to suppose that all (natural) genera will be found to have well-marked attributes both common to and peculiar to all their members.

(iv) The "natural" affinity based only on all the parts of an organism may be very misleading at the specific and generic levels. Geographical or palaeontological evidence may reveal much convergence and lead to a considerable regrouping of

forms; and when, as so often, such evidence is lacking, we are left with the uncomfortable feeling that the best we are able to do does not reflect the phyletic situation.

These points require further consideration.

Discrete Groups

The use of only discrete groups, discontinuous one from another at each level of the hierarchy, was justified as long as it was believed that all groups were in fact discrete, and that, in particular, each species was as it had always been since the Creation, or at most, as Linnaeus came to believe, had generated a clearly marked natural group of distinct forms. Such an attitude was of the greatest use as Pirie (1952) has pointed out, when the first necessity was to explore, describe, and provide means to identify the enormous wealth of material that had begun to be discovered by the immediate predecessors of Linnaeus. Good keys, clear definitions, constant diagnostic characters, and an easily memorised, simply constructed, and unambiguous reference system were the great requirements and Linnaeus was perhaps the most generally successful in producing them. To do so is still an important function of the taxonomist.

The concept of the species as the lowest category in biological classification was based on Aristotelian logic and philosophy, with its notions of real substances each with a nature and essence characteristic of its species (Crombie, 1950), and was reinforced by the notions of special creation and fixity of species, in such a way that a system of discrete groups appeared not only useful but completely sufficient in theory for classifying organisms. The establishment of the theory of evolution produced no great immediate upheaval of taxonomic theory and practice merely because the fossil record was (and in large measure still is) too fragmentary to enforce a taxonomy of continuity. The few fossils known could easily be classified into discrete species. Moreover, the study of geographical variation was not yet so advanced as to intrude so intractable a phenomenon as the ring-species (Mayr, 1942; Stresemann and Timoféeff-Ressovsky, 1947; Cain, 1954*a*, 1955) into taxonomic discussions. At the present day, ring-species and continuous fossil series are well known and cannot be ignored. Continuity cannot well be expressed by a system using only discrete classes and the relation of inclusion of one group within another.

Phyletic Lineages

Simpson's discussion of the species concept (Simpson, 1951) leads him to consider that "a phyletic lineage (ancestral-descendent sequence of interbreeding populations) evolving independently of others, with its own separate and unitary evolutionary role and tendencies, is a basic unit in evolution. The genetical definition [of species] tends to equate the species with such an evolutionary unit," at least at any one instant in time. After discussing the extreme difficulties that may beset the palaeontologist in trying to decide whether a particular series of samples of fossils is an example of such a single line, Simpson considers the purely taxonomic difficulties that arise when such lineages can be identified and are found to branch. If a chronological series of morphologically intergrading forms—*A, B, C*—forks, producing two others, *D, E, F*, and *G, H, I*, it may be impossible to draw any non-arbitrary line separating *C* from *D* and *G*, yet *D* and *G* may clearly be good species. Moreover, morphological characters do not alter in different lines at the same rate, and they must be taken into consideration in delimiting the species. If *A, B, C, D, E*, and *F* are all extremely similar, while *G, H*, and *I* show marked changes, it might well be advisable to classify the former as a single species, and *G, H* and *I* as separate ones, although *G* is as continuous with *C* as is *D*. In such situations, as Simpson remarks, the frequent occurrence of breaks in the record is very useful since, not having been put there by the

taxonomist, they are "non-arbitrary" and one can reasonably use them for delimiting species. "This is still a separation in what *was* a continuum, but it is non-arbitrary (by the special definition of that word in this paper) as regards the actually available materials being classified." Exactly the same considerations arise if the simple or branching lineage is diverse enough to be considered a genus. Where shall it be cut off from the earlier forms and how far up each branch shall it extend? Moreover, in the case of the genus and higher categories, questions of polyphyly may also arise; these are considered later.

Comparative and Breeding Data

The justification for the use of morphological data and criteria in delimiting species and genera is that (i) it allows the inclusion in the taxonomic hierarchy of forms known only from a few morphological characters (the absolute minimum of taxonomic evidence) and (ii) morphological criteria are the main example of the only class of criteria available at all in grouping asexual forms at the species level, and in classifying all phyletic lines into the higher taxonomic categories, i.e. the genus, and its sub-divisions, upwards.

There are two distinct activities of the taxonomist which are often confused; one is the recognition of phyletic lines and their separation one from another at any moment in time, and the other is the grouping of these phyletic lines according to their "natural affinities" to produce a natural classification which will show as far as possible the course of evolution in each group. The difference is indicated in Figure 1. In Figure 1*a* are represented a series of samples which on their time-relations and other evidence can be arranged in the phyletic scheme shown, which indicates only what phyletic lines are to be recognised and their time-relations—that is, only the evolutionary topology of this group of forms. In Figure 1*b* is shown the same set of samples arranged to show *both* their phyletic relationships *and* their degrees of general morphological resemblance, or "affinity." The "natural" groups are not those shown in Figure 1*a*.

Clearly, then, the delimitation of phyletic lines as different branches from other lines, and their grouping into the natural groups of the taxonomic hierarchy are not the same activities. The assumption that the phyletic lines must be recognisable by the same criteria as is any other natural group in the taxonomic hierarchy (an assumption that lies behind any attempt to use nothing but morphological criteria for the whole of taxonomy) cannot be maintained; it is a relic of a pure Aristotelian mode of classification, and was in fact abandoned when Linnaeus, like John Ray before him, characterised species as breeding true, thereby emphasising the reproductive criterion, at the expense of the morphological. If purely morphological criteria had been employed by Linnaeus at the species level as well as elsewhere in the hierarchy, he would have been forced to separate the sexes of many species, which may differ far more than either does from the same sex of closely related species (Cain, 1954*a*). The same is true if purely physiological, ecological, or ethological, as well as morphological, characters are used. But, on the other hand, as Simpson has pointed out (1951, p. 287), *purely* morphological criteria are not used in classification. There is always some weighting of characters according to their *taxonomic importance,* not only at the species level but higher in the hierarchy as well. "Characters are always selected, weighted and interpreted." They are not merely taken at their face-value.

There is, therefore, a fundamental difference in taxonomy between *breeding data,* and all others (usually morphological) which can be grouped together as *comparative data.* The first (or indirect evidence bearing on them) are used to establish what are the phyletic lines in any sexually reproducing group, how they are interconnected and especially how

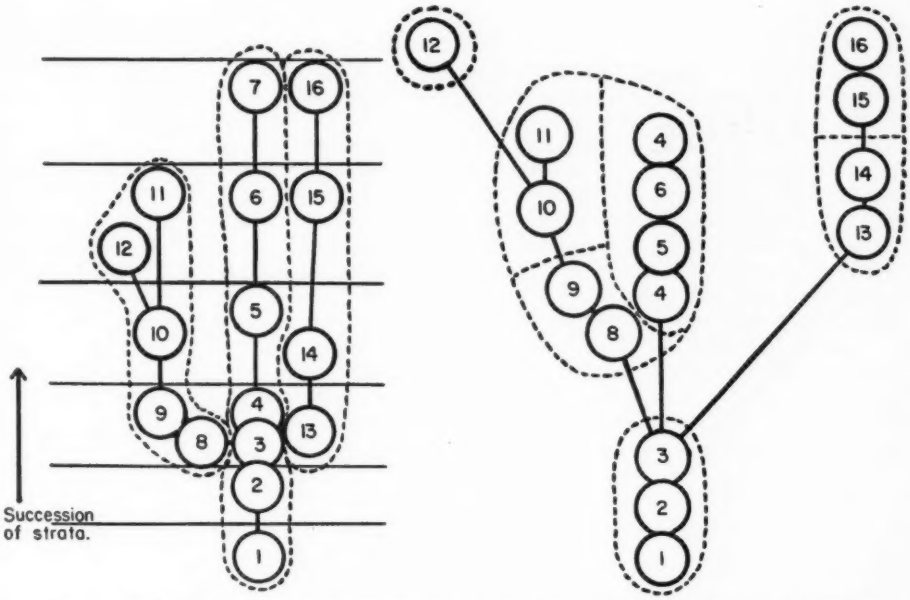

FIG. 1*a* (*left*). A number of samples of closely related fossils arranged to show their location in the strata and their presumed lines of descent.

FIG. 1*b* (*right*). The same samples as in Figure 1*a*, but arranged to show both their lines of descent and their degrees of over-all affinity.

many are distinct at any one time. They are the real basis for the construction of diagrams such as Figure 1*a*. The breeding data allow us to determine the *biospecific distinctiveness* of each separate phyletic line at any one time, and its origin from an earlier line. Of course, it is not necessary to insist on *complete* lack of crossability (Mayr, 1942) before one population can be regarded as biospecifically separate from another (Simpson, 1951).

Comparative data, on the other hand, give us a measure of the similarities and differences between any two known forms —broadly speaking, their "degree of affinity." From them we can decide whether the amount of change in one phyletic line over a given period is less than, more than, or the same as, in some other line. They do not necessarily, merely as such, give us any information on breeding since, as already mentioned, they may well separate sharply stages in the same life-history, different sexes of the same species, or different polymorphic individuals of the same population. But it is true that in the absence of breeding data, comparative data (often purely morphological) may be all that are available, and may often be used with fair certainty to indicate what are separate, non-interbreeding populations. If it were true that all phyletic lines were morphologically (or physiologically or ethologically) distinct at each instant in time, and each had unique characters by which it could be recognised, then comparative data would always be sufficient for distinguishing phyletic lines as well as for grouping them, and the same data would suffice for constructing both Figures 1*a* and 1*b*. Unfortunately this is not so. Perfectly good species, biospecifically separate at the present day, may be virtually indistinguishable mor-

phologically, and forms in one group which by observed intergradation must be ranked as only subspecies may be as distinct morphologically as good species in related groups. Comparative biochemical, physiological, or ethological evidence suffers from exactly the same limitations as comparative morphology, and Mayr has therefore rightly said that Wilhelmi's "physiological" definition of the species in helminths (Mayr, 1942, p. 117) is simply the old morphological definition in a modern disguise. Biospecies are phyletic lines of sexually reproducing forms considered at any one time; the evidence necessary to establish their separateness one from another is that they are nearly or completely non-interbreeding populations (see Cain, 1954*a*, p. 94) and no other form of evidence is a completely sufficient substitute in all cases. But only comparative data can be used through the rest of the taxonomic hierarchy or for agamospecies. As long as it could be believed either that the species was only the lowest level in this hierarchy, or that it was a separate-breeding entity but invariably delimitable by comparative studies, then comparative data were sufficient for all taxonomic purposes. Now, it must be admitted that the homogeneity of taxonomic criteria is gone for good. At the level of the phyletic line and biospecies, the criterion relates to interbreeding and all evidence must be graded in taxonomic importance according to its usefulness in providing relevant inferences. But above the level of the biospecies, only comparative data can be used, and they are the basis of the rest of the natural classification.

The relations between breeding criteria, comparative criteria, and genetical data are not simple, and have been the cause of some confusion. It has been said, for example, that genetical data or criteria are useless in taxonomy above the level of the species. But few characters could be more genetical than the mode of sex-determination in most organisms; the fact that in the class Aves the female is the heterogametic sex, whereas it is the male in the class Reptilia as well as in the Mammalia is of undoubted taxonomic value. A general resemblance in chromosomal morphology between two groups could equally well be described as a genetical observation of taxonomic value. But clearly, in these two examples, genetical data are valuable only as comparative data and are on exactly the same footing as morphological, psysiological, or ethological comparative data. When, however, one form is found purely by examination of their chromosomes to be a simple tetraploid of another, we are immediately put in possession of a most important fact which instantly indicates

(i) the closeness of their relationship;
(ii) the almost certainty that the tetraploid arose from the diploid—i.e. the direction of evolution;
(iii) the mechanism of the change, and
(iv) the certainty that the two forms now constitute reproductively separate populations.

Although the data are purely comparative, they permit an inference about the reproductive situation so highly probable that most workers might think it unnecessary to get data on actual crossability in the field. This is a particularly clear instance of weighting for taxonomic importance—in this case, simultaneously for inferring whether a population is part of a phyletic line separate from any other existing at the same time, and how close it is to its nearest relative and what is the phyletic relation between them. In this example, the weighting is so heavy that comparative data reach the same order of importance as breeding data in assessing the separateness of phyletic lines.

Further, Rollins (1953) has pointed out that data derived from hybridisations can be valuable in determining relationships. If two species can hybridise to produce fertile offspring (even if they never do so in the field) the fertility indicates that they are more closely allied to each other than either is to any other species with

which they produce sterile or inviable hybrids. Here, breeding data are of use, not in separating phyletic lines, but in grouping them together. However, such data must be interpreted with caution. The genetical differences between interfertile and intersterile forms need not be a measure of their overall affinities but merely an indication of whether or not they have built up special barriers. Isolating mechanisms (Dobzhansky, 1951) can be evolved on particular occasions; consequently, distinct but widely separated populations may never have built up barriers, since they have never met, yet may be completely interfertile, while very closely related and similar forms which have met along a broad front for a long time may come to overlap as good species, and never hybridise in the field. An example of this has been worked out by I. C. J. Galbraith (in preparation) in the superspecies *Pachycephala pectoralis* and is briefly discussed by Cain (1954*a*).

Forms which reproduce totally asexually (agamospecies) can be grouped only on comparative data; no others are available (Cain, 1954*a*, p. 98). If no such forms existed, we could say that criteria of separateness at the specific level were based on breeding data, at all other levels on comparative data, but this pleasant correspondence simply does not hold. In any case, it does not hold for the delimitation of successive forms (palaeospecies) in a single lineage.

The Palaeospecies

The palaeospecies has been defined as a piece of a single phyletic line arbitrarily delimited as a separate species from the precedent and subsequent portions. It is the result of an unhappy attempt to impose a taxonomy of discontinuous groups on a continuous series (Simpson, 1951; Cain, 1954*a*, Ch. 7). If several good species of a group are known to have coexisted at any one time, then the sort of differences that are seen between them are regarded as probably indicating specific distinctiveness in close relatives as well, including successive populations in a single phyletic line, which can therefore be divided up arbitrarily into pieces, the forms in the centres of each of which differ approximately as much as do different lines coexisting at the same time. But this is to apply comparative data at the species level, and as just shown, what is required at that level for sexually reproducing forms is breeding data. It is impossible to obtain data which will allow one to decide when a given phyletic line has changed so much that the latest descendent population considered could not interbreed with the earliest one even if they could meet. It is impossible because (i) the ancestral population will have perished, so that no actual trial can be made, and (ii) as seen above, comparative data are no sure guide to the possibilities of interbreeding, even between contemporary forms. The analogy with differences between known good species is therefore uncertain; far less difference might be produced between reproductively separate populations than is actually found to occur between the known good species related to them, and conversely, in a particular line there might have been considerable change in morphology without reproductive incompatibility.

As long as biospecies and palaeospecies are both called species in some sense, the species-level in the taxonomic hierarchy is not homogeneous (even if asexual "species" are excluded) as Simpson has emphasised (1951). It will contain, without differentiating between them, both groups that are sections through different phyletic lines, delimited from each other on breeding data, and groups that are successive pieces cut out of phyletic lines, no doubt at any one time separate from all other phyletic lines then existing, but each delimited from its predecessor and successor purely on the basis of comparative data. It is standard practice to refer to both entities by specific names, each a binomen formed in accordance with the International Rules of Zoological Nomen-

clature, and no proposal for reform that requires any considerable departure from this practice can be considered practicable. The relations between these two sorts of taxonomic "species" are shown in Figure 2. *A*, *B* and *C* are biospecies, portions of different phyletic lines, distinguished primarily by lack of crossability (Mayr, 1942, p. 119) and —in this and most other examples—morphologically as well. Degrees of morphological difference between *A*, *B* and *C* being used as a yardstick, the phyletic line *ab* is divided up into sections *C*, *D*, *E*, *F*, etc., which intergrade and are palaeospecies. When good biospecies are morphologically well-nigh indistinguishable, as in the now famous case of *Drosophila pseudoobscura* and *persimilis*, or when morphological characters (or others) clearly do not keep step with reproductive distinctiveness (as would be the case if, in Figure 2, forms *L* and *M* were reproductively separate but so similar to *N* as to necessitate their being ranked as subspecies of it on comparative data), the classification of a given group into species on breeding data may be frankly incompatible with any classification on comparative data.

Figure 2 helps to elucidate the relationships between the phyletic line, the biospecies, and the palaeospecies. Different phyletic lines that coexist at any one time are, as Simpson says, separate evolutionary units; a time-section, such as *xy*, reveals them as separate biospecies, reproductively distinct. It is not, therefore, wholly correct to say (Simpson, 1951, p. 289) that the "genetical" definition of the species tends to equate it with a single, unitary, phyletic lineage. Strictly, the reproductive definition equates it with a single lineage considered at a single instant, or rather, during a short period, the time-quantum of the biospecies (Cain, 1954*a*, p. 102) during which interbreeding is possible. But this definition, consistently used, would leave us no grounds for not dividing up every lineage by time-quanta wherever possible, e.g. into annual sections for forms with a single breeding season each year, and naming every division as a different species. In fact, the extreme general similarity seen in those populations within a single phyletic line that are very closely adjacent in time, leads us to believe that all the individuals within them could have interbred freely if only they could have coexisted in time. But this is to introduce comparative criteria as a substitute for strictly reproductive criteria which, by the nature of the case, cannot be applied. The palaeospecies, therefore, must be characterised as a time-series of populations known (or believed) to be connected successively by descent, reproductively separate from all other forms coexisting during the same period, and sufficiently homogeneous on comparative criteria to be included under a single specific name. It is not only the result of an attempt to impose a taxonomy of discontinuous groups on a continuous series, but also an attempt to use simultaneously two different sets of criteria, reproductive and comparative. If all that were known of the forms represented in Figure 2 were a few specimens each of *A*, *C*, *E*, and *N* (say), only comparative data could be used to classify them at all. Nevertheless, if sufficient information were to come to light later to make pos-

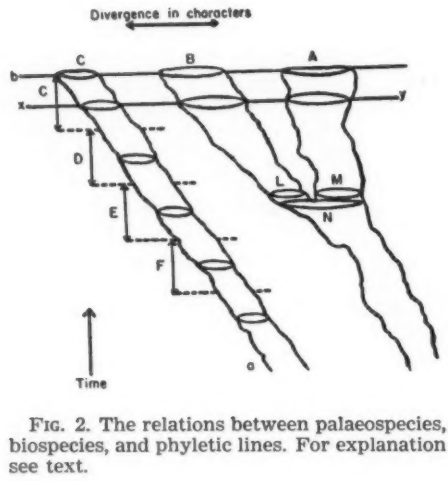

FIG. 2. The relations between palaeospecies, biospecies, and phyletic lines. For explanation see text.

sible the construction of Figure 2, the classification founded purely on comparative data must be corrected by reproductive criteria, or by comparative data weighted not purely comparatively but in relation to their value as indicators of the reproductive situation.

In fact, as the amount of knowledge about a group increases, there is a change in the criteria that can be applied to it. In a very poorly known group, only comparative data can be obtained, and they may be sufficient only to indicate in the broadest way the general affinities of the various forms, without giving the slightest clue to their exact phyletic interrelationships. As more data become available, it may be possible to obtain some evidence, direct or indirect, on the phyletic situation, and in part at any rate to construct such a diagram as Figure 2. But as soon as this happens, the natural arrangement produced solely on comparative data must be corrected to correspond as far as possible with the phyletic data, and this correction may, in fact, involve abandoning the first-produced natural arrangement.

Taxonomic Importance

From the foregoing discussion, it is obvious that taxonomic importance can be based on very different criteria in different categories.

(i) At the biospecific level, data are graded according to their reliability in providing evidence of actual or potential crossability, when the separation of forms into biospecies is being carried out.

(ii) At the species level for all kinds of species and in all higher groupings, once the different biospecies have been distinguished, the degree of resemblance in all characters is used to produce natural groups. This general degree of resemblance and differences is presumably what Linnaeus would have called affinity.

But lastly,

(iii) All other evidence that bears in any way upon the actual evolutionary sequence of events is used to correct the arrangement made on the basis of plain affinity by distinguishing affinity due to close evolutionary relationship from that due to convergence.

This last raises an important point, clearly stated by Simpson (1945) when he says that classification must be based on phylogeny but cannot express it. The classifications used to-day must not include together in the same natural group forms whose resemblance is due only to convergence, if thereby they are separated from those forms to which they are really related. But when, as is usual, the detailed phyletic history within a group is not known, the classification used has no phylogeny to express, and when it is known, the categories available are quite inadequate to express it—only a diagram such as Figure 2 can do justice to it, and not even diagrams like these are adequate for ring-species, sibling species, or in general any forms in which morphological and reproductive distinctness do not go hand in hand. The most that the ordinary classification can do is avoid disagreeing with the phylogeny of a group as far as known.

But even this statement requires qualification. As Arkell and Moy-Thomas (1940) have pointed out, examples are known of phyletic lines, closely related and evolving in parallel, in which the characters of extreme phyletic importance that distinguish the lines are inconspicuous compared with the resemblances between contemporary forms. Judged on pure affinity, the genera (or other groups above the species) must be horizontal, not vertical, the more so because there are forms which can readily be included in such genera but whose phyletic position is uncertain, so that they cannot be assigned to one or other phyletic line. Here, different species of one genus clearly have arisen from different species of the immediately preceding one. However, it is usually considered sufficient to make sure that no genus as delimited is derived from two or more preceding genera. In gen-

eral, a group in one category is polyphyletic if it arises from more than one of its own or a higher category.

The sort of evidence that can be used to correct a classification based on pure affinity varies greatly from group to group. Two examples from birds, actually just below the generic level, may be of interest. The well-known rules of geographical variation due to Bergmann and Gloger lead us to expect that subspecies, and often closely related species also, in cold damp areas will be larger and darker than their relatives in hot dry ones. In the fruit-pigeons of the genus *Ptilinopus*, there is a striking similarity between two geographical representatives, *Pt. regina* of Australia and the Lesser Sunda Isles, and *Pt. roseicapilla* 35° of latitude away, in the Marianas, and it has been suggested that they are closely allied in spite of the enormous distance between them which is occupied by related but less similar forms. Suspicion is aroused when we find that the resemblance extends only to the southernmost subspecies of *Pt. regina*, i.e. the subspecies in the coolest and wettest part of the range, and that these two forms are the furthest from the equator, to south and north, respectively, of all the forms in the species-group. It is very likely indeed that much of the resemblance between these forms (although not all) is due to the convergent effects of selection by similar climates. At all events an arrangement placing *Pt. roseicapilla* next to the southernmost subspecies of *Pt. regina* is almost certainly not sound phyletically (Cain, *Proc. 8th Pacific Sci. Congr.*, in press).

Geographical evidence is often of value in detecting convergence irrespective of geographical rules and similar regularities that suggest convergent selection. The genus *Myiagra* comprises a very natural group of flycatchers distributed from the Lesser Sunda Isles to Tasmania, the Marianas, and Samoa. All are geographical representatives except that three overlap in Australia and southern New Guinea and two occur in Fiji. The mountain-forest form in Fiji, *M. azureocapilla* is unique in that the male has a bright blue cap. It was duly separated as the genus *Lophomyiagra*. But in all other respects it agrees so closely with the Samoan form next door that they must be closely related, and the Samoan bird, except that it is hen-feathered, is a quite typical member of the genus. The genus *Lophomyiagra* cannot be upheld. More interesting is the remarkable resemblance between the Samoan form, *M. albiventris* and that in the Lesser Sunda Isles, *M. ruficollis*. I showed this genus recently without geographical data to a class in taxonomy and told them to group it by pure affinity; all agreed in placing *ruficollis* with *albiventris* and *azureocapilla*. But by examining ranges they found that its affinities must be with its nearest neighbours in the Tenimber Isles and northern Australia, which do indeed resemble it, and that it is cut off from *albiventris* by the full east to west range of the genus (about 4000 miles) and by ten other forms distributed in between. The chances that these two are really more closely allied phyletically to each other than each is to its neighbours are extremely remote.

In a similar way actual sequences of fossils, when available, can be used to correct a classification and show what characters do indicate separate phyletic groups. The classic example is the horse and cow. With the knowledge available in his time, Linnaeus was probably right to group them together. The possession of one digit or two on each foot, for example, need not be thought of great importance; after all, pigs have four and cows two, yet they are obviously allied. Yet the known fossil history shows clearly that this trifling character is indeed of great importance as an indicator, separating the Paraxonia from the Mesaxonia. Here is yet another meaning of taxonomic importance, with its own separate criteria. This by no means exhausts all the meanings (Cain and G. A. Harrison, in preparation).

Characteristics of the Genus

From what has been said above, it is obvious that the present idea of the genus differs somewhat from Linnaeus's. Its constituents are far from unitary, equivalent and monotypic. The biospecies itself, the best-defined sort of species, is unitary in a reproductive sense, as Simpson says. But it often cannot be described by a single monotypic description when it includes considerable geographical variation, and in the case of extreme siblings may not be separable on morphological characters (see, e.g., Cain 1954*a*, Ch. 6). Reproductive distinctness does not always correspond to morphological distinctness —i.e., pure affinity may be misleading. Agamospecies and successive palaeospecies in a single line must be distinguished on comparative criteria, since for them nothing else is available. The genus is the lowest obligate category for which invariably only comparative data, corrected as far as possible from all data bearing on actual phylogeny, are available. It is a natural group of species, monophyletic in the sense explained above, and arbitrarily delimited at any one moment in time when either it merges backward and forward into phyletically continuous forms, or phyletic lines exist halfway in their affinities between it and a contemporary related genus and could be equally well included in either. Since the entities it contains are so far from being monotypic units, it is not surprising that some genera are known which are clearly natural groups yet cannot be diagnosed at all, since every character confined to them is lost or modified in one or more forms, the remainder of whose characters suffice to establish their membership in the group. An example is the genus *Ptilinopus* (Cain 1954*b*). Some examples in flowering plants are given by Sherff (1940). Since, as remarked above, there is no evolutionary law quantifying divergence, there is nothing to prescribe the degree of difference which calls for generic separation, as against familial or ordinal. Ranks other than the individual, the biospecies at any one instant in time (and not even then if there is continual hybridisation), and that containing all living things, have only a positional value (Cain 1954*a*).

We may agree with Svenson that most of our genera are not natural units but merely represent a stage of classification above that of the species, in the sense that many are merely easily keyed-out groups and thus artificial, while many more are "purely natural" because no data bearing on phylogeny are available. This must very often be the case in insects, for example. The theory of evolution has indeed not eased the problem; nor should it, since it has rightly brought out the difficulty of applying a taxonomy of discrete groups to a dendritic assemblage in which every twig and branch are ultimately interconnected. We cannot hope to remove the accepted taxonomic system, which is far too firmly entrenched, yet a taxonomy of continuous groups should be designed, for maximum efficiency, only with regard to the problem, not to history as well. We need to express *relationships* such as those between agamospecies and their parent biospecies, or two sibling species, or the various forms in a ring-species, when necessary, while retaining the magnificently non-committal inclusiveness of the Linnean categories for poorly known forms. Moreover, as Linnaeus himself pointed out, the reference system must be such that it does not change as ideas on the interrelationships of particular groups change; this immediately means that the names of groups must remain stable—i.e. that we should be able to move them about in our schemes as units, which more or less imposes the view of them as discrete.

The key to a solution lies in the word "relationships." It is noticeable that all the recent developments at or about the specific level that have been proposed are designed to introduce relationships. Examples are the cline (Huxley, 1938), the subspecies as a geographical race (not in its earlier meaning as merely a well-marked form within the species), the su-

perspecies and its predecessor the *Artenkreis* (Mayr, 1931, 1942), the ecotype and ecospecies (see Baker, 1952; Valentine, 1949), the agamospecies, morphospecies, and palaeospecies (Cain, 1953, 1954*a*), the sibling species (Mayr, 1942), and the sets of symbolic prefixes proposed by Kiriakoff (1948), and Huxley (1942). Such proposals are characteristic of the "New Systematics." Of particular interest is the admirably designed set of terms proposed by Gilmour and Gregor (1939) and elaborated by Gilmour and Heslop-Harrison (1954). I cannot agree with the latter when he states (1953) that the aims of "classical taxonomy" are to describe all existing "kinds" of organisms, to classify them according to their resemblances and differences, and to name them according to a body of internationally agreed rules, contrasting this with "experimental taxonomy," the aims of which are to identify evolutionary units, and by experiment to determine their genetical inter-relationships and the rôle of the environment in their formation. Surely there is no distinction, or rather it is the distinction between the α-taxonomy of groups so far only inadequately worked, and the ω-taxonomy of really well-worked ones. Surely all taxonomists aim at doing both as far as their material and circumstances will allow. The problem now before us all is to find the best method for supplementing the classical taxonomy and correcting it, so that, as information becomes available, it becomes based upon everything that is known about each group, and allows the maximum number of generalisations to be made about the course of evolution.

Summary

1. The genus as used by Linnaeus was the smallest "kind" or "sort" recognisable without much expert study. Each genus was a natural, discrete group, separable from those most closely allied by some definite attribute, recognisable when all the species in it had been discovered, if not before.

2. The species was regarded as unitary but still named by differentiation within the genus. Species were monotypic, morphologically distinct, and equivalent, no different kinds of species being recognised.

3. The same sort of comparative criteria could be used for distinguishing both species and genera, except that for species the criterion of breeding true had been accepted in addition for some time.

4. Examination of criteria now used leads to a sharp distinction being drawn between *breeding data* and *comparative data*. Confusion has arisen because the latter must often be used for want of direct evidence in place of the former, and genetical data may appear under either heading. Moreover, comparative data are not always consistent with breeding data and may be contradicted by them.

5. A review of the interrelationships of different sorts of species and the evolutionary tree shows that the genus cannot now be regarded as a naturally discrete group either in relation to its ancestors and descendants, or at any one time. It is not necessarily definable by one single peculiar attribute, nor are its constituents monotypic, equivalent, essentially merely subdivisions of it, or themselves wholly discrete. It is monophyletic, but purely positional in rank, and a collection of phyletic lines, not an entity subdivisible into species.

6. Only comparative criteria are applicable at the level of the genus (and other higher categories). Within the genus, they only are applicable to agamospecies and successive palaeospecies, while breeding criteria are appropriate for biospecies.

7. The available taxonomic information varies greatly from group to group, and a comprehensive classification must include both poorly known groups to which only comparative criteria can be applied, and very well-known ones in which phylogenetic and biospecific (breeding) criteria can be used with some approach to certainty.

8. The obvious course is to continue to

use the Linnean system as a universal basis but to supplement it as information becomes available by indications of the relationships between the constituents in each group. The whole trend of the "new systematics" is toward this supplementation by means of relators, words or symbols specifying relationships and mitigating the discreteness of the groups in the Linnean system.

9. In view of the differences between Linnean and present-day taxonomy, it is worth while considering whether the latter can still be said to be Linnean.

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Geographic Variation and the Subspecies Concept in Butterflies

NICHOLAS W. GILLHAM

RECENTLY two papers have been published by lepidopterists in defense of the subspecies concept. These papers are only two of the many that have argued the pro's and con's of a trinomial system for zoological nomenclature in the last few years, but they were of particular interest to me as a lepidopterist. After reading them, it seemed to me a good idea to take stock of some of the more exhaustive studies that have been published on butterfly subspeciation. Mayr, Linsley, and Usinger (1953) characterize the subspecies as "a geographically defined aggregate of local populations which differs taxonomically from other such subdivisions of the species." This definition leaves us with the question of whether or not the subspecies effectively describes the geographical variation of the component populations of a species. Are subspecies really "geographically defined aggregates" when several different characters are analyzed carefully? The study of this question requires abundant evidence, and I have attempted to gather this from the more detailed, mostly statistically documented contributions on butterfly taxonomy. It soon became evident that only those papers treating variation of individual characters, over and above the usual definition of subspecies entities, would furnish readily available information on this subject.

Before entering into a discussion of individual papers which consider geographic variation, it seems pertinent to discuss briefly the two papers by lepidopterists in support of the subspecies concept. Van Son (1955) limits his subspecies to "population variations conditioned by geographical or host isolation." Thus, for van Son, the subspecies includes strictly allopatric aggregates of populations that differ taxonomically from other such aggregates. This is different from the definition of Mayr, Linsley, and Usinger in that it eliminates from consideration groups of populations among which there is a certain amount of contact. Van Son exemplifies this concept by a discussion of *Papilio ophidicephalus* Oberthur (Papilionidae) and its subspecies (discussed in further detail below).

The second paper is by Fox (1955), who also feels that the use of the trinomen should be restricted, but not eliminated entirely. He finds in his work on butterflies of the family Ithomiidae that the subspecies is useful in describing populations that differ from one another in color and pattern, but which are otherwise apparently morphologically identical. Characteristics of pattern and color in this group appear to be strongly influenced by mimicry, and Fox states that in his experience he has not noted any appreciable non-concordance of geographic variation. This latter statement is essentially in answer to the thesis of Wilson and W. L. Brown (1953) that the geographical variation of independent characters tends to be discordant in some degree. Unfortunately, Fox's paper can be evaluated only as a personal opinion, since he neither presents any specific examples from among the ithomiids nor cites any references to such examples.

Variation in Incompletely Isolated Populations

Most continental butterfly populations may be presumed to be incompletely isolated, with the exception of some isolated

montane and bog populations and a few others very specific in their environmental requirements.

Clinal variation. Many of the subspecies that have been named in the butterflies appear to represent segments of color or pattern clines. Ehrlich (1952) reports that the four Nearctic subspecies of *Erebia rossii* (Curtis) (Satyridae) appear to grade into one another clinally when enough populations are sampled. F. M. Brown (1953*a*) in a statistical study of geographic variation in *Oeneis uhleri* Reakirt (Satyridae), shows that subspecies *uhleri* (central Colorado and Wyoming) is significantly different from subspecies *varuna* Edwards (Alberta and Saskatchewan) in three separate characters. However, two of these three characters, maculation and size, appear to show clinal variation from north to south. One gets the definite impression from Brown's data and figures that significant differences would be obliterated if he had been able to obtain samples from intermediate localities.

Avinoff and Sweadner (1951) in a monographic treatment of the Central Asiatic satyrid genus *Karanasa*, describe a number of character clines. Perhaps the simplest of these concerns the species *pamira* Grum-Grshmailo. This species occupies a Y-shaped distribution along the eastern and southern sides of the Amu Daria drainage basin. The cline involved is one of color, with the lightest race (*pamira*) at the northern extreme and the darkest race (*haslundi* Avinoff and Sweadner) at the southern end.

Avinoff and Sweadner have separated this species into six subspecies. Five of these fall directly along the color cline and represent segments of it. The sixth is slightly off to one side geographically, but is morphologically intermediate between the two subspecies nearest it. One wonders if a simple description of this cline would not have described the variation better than does the designation of a whole series of new subspecies. The problem is repeated in other species showing more complicated variation, and Avinoff and Sweadner meet it by introducing a pentanomial system, including categories ranging from natios to superspecies. In a review of this paper, Munroe (1953) suggests a much more reasonable classification and points out that "the struggle to characterize the elusive and inconstant differences of [the species complexes] *'wilkinsi'*, *'leechi'*, *'intermedia'* and *'josephi'* seem to me to be typical of the sort of difficulty one often encounters in the initial stages of investigation of a species problem, when one is grappling with what eventually prove to be imaginary, or at least intraspecific, differences." The problem would have been simplified even further had the authors not tried to give every population or group of populations a formal taxonomic "handle." In the case of *Karanasa*, the pentanomial categorization within the species stands as the clearest possible warning to taxonomists.

Discordant variation. The question of whether or not independent characters show discordant variation is crucial to the geographically defined subspecies of Mayr, Linsley, and Usinger, and of all other systematists who support this concept. Wilson and Brown (1953) cite a number of examples in diverse groups of animals showing that genetically independent characters tend to vary discordantly. Partition of a species into geographical races cannot indicate discordant variation without granting undue biological and taxonomic significance to one or a few characters, and suppressing or concealing characters that are merely less conspicuous to a human observer. In butterflies the tendency has been to name groups of populations differing from other groups within the same species in characters such as size, pattern, and general coloration. As will be shown in several of the examples to be discussed, color and size are often discordant in their variation, and individual components of the color pattern are discordant among themselves.

In 1941, Davenport published a revision of the Holarctic satyrid genus *Coenonympha*. One of the species, *C. tullia* Muller, ranges over most of this region

and shows a great deal of variation. As a consequence of this, many subspecies have been described. F. M. Brown (1955) takes a segment of the Nearctic population and designates it as species *inornata* Edwards, thus raising *tullia* to superspecific rank. He then proceeds to make a statistical evaluation of a number of characters having to do with size, pattern and color in relation to four established races of *inornata*. *Mcisaaci* dos Passos occurs on Newfoundland; *nipisiquit* McDunnough is known from Bathurst, New Brunswick; nominotypical *inornata* ranges from eastern Quebec westward to Saskatchewan; and *benjamini* McDunnough occurs from south-central Canada southward to South Dakota. In Figures 1-7 seven of the characters studied are plotted geographically against the "recognized" borders of the four subspecies. Where one type of shading ends and another begins, a statistically significant difference is to be found between adjacent populations (these are based on Brown's analysis). Similar types of shading indicate groups of populations which are similar for the particular character concerned. A glance at these maps shows that significant differences in characters are rarely concordant with subspecies boundaries. In addition the characters analyzed show a large amount of discordance with one another. For each one, a different alignment of subspecies could be recognized, and it becomes obvious that the conventional trinomen cannot describe this variation properly. I have included one plot (Fig. 8) which shows the places from which Brown's statistically treated samples came. It can be seen from this that more samples from eastern and central Canada would be highly desirable. The east-west junction at Lake Superior really reflects only a broad gap in the sampled range. The northern boundary line of *benjamini* also suffers in this respect.

The cases of *mcisaaci* and *nipisiquit* deserve special attention, since at first there appears to be some reason for considering them distinct subspecies. In his geographic plots, Brown shows that *mcisaaci* differs significantly from central Quebec and New Brunswick populations in four characters. However, in his data he treats a short series from Bradore Bay, Quebec, which is just across the Strait of Belle Isle from Newfoundland. This series is not included in his geographic plots, but it strongly indicates that examination of more populations from eastern Quebec would show the mainland series to grade into the Newfoundland series, as Brown himself intimates (p. 370). Furthermore, examination of the data for the individual Newfoundland populations shows some to be different from others by an order of magnitude that Brown considers significant when differentiating mainland samples from the lumped Newfoundland data. *Nipisiquit* differs significantly from Quebec and Newfoundland material in three characters, but this subspecies is based entirely on topotypical (Bathurst) material. Brown (*in litt.*) remarks that diligent search has revealed no other colony. However, further collecting in eastern Quebec is needed in order to establish whether this character concordance is real or merely apparent. In any case, if one applies this three-character standard for *nipisiquit*, then one would presumably be justified in uniting *benjamini* and western *inornata* into a single subspecies; this would cut right across the subspecies boundaries presently recognized on the mainland. As a matter of fact, two of the three characters distinguishing *nipisiquit* are those serving to lump *benjamini* with western *inornata*.

LeGare and Hovanitz (1951) have published a study of genetically based color variation in California populations of *Euphydryas chalcedona* Doubleday and Hewitson (Nymphalidae). This has previously been discussed by Wilson and Brown as a case of discordant variation, and it is pertinent in the present review. The data of LeGare and Hovanitz show that adult color, larval color, and size are poorly correlated geographically. Furthermore, the varying amounts of yellow and red pigment in the wings appear to show no correlation. Although most of

the samples analyzed fall within the range of the nominate subspecies, the data may be extrapolated to cast a large measure of doubt on the many described subspecies of *chalcedona* from other localities.

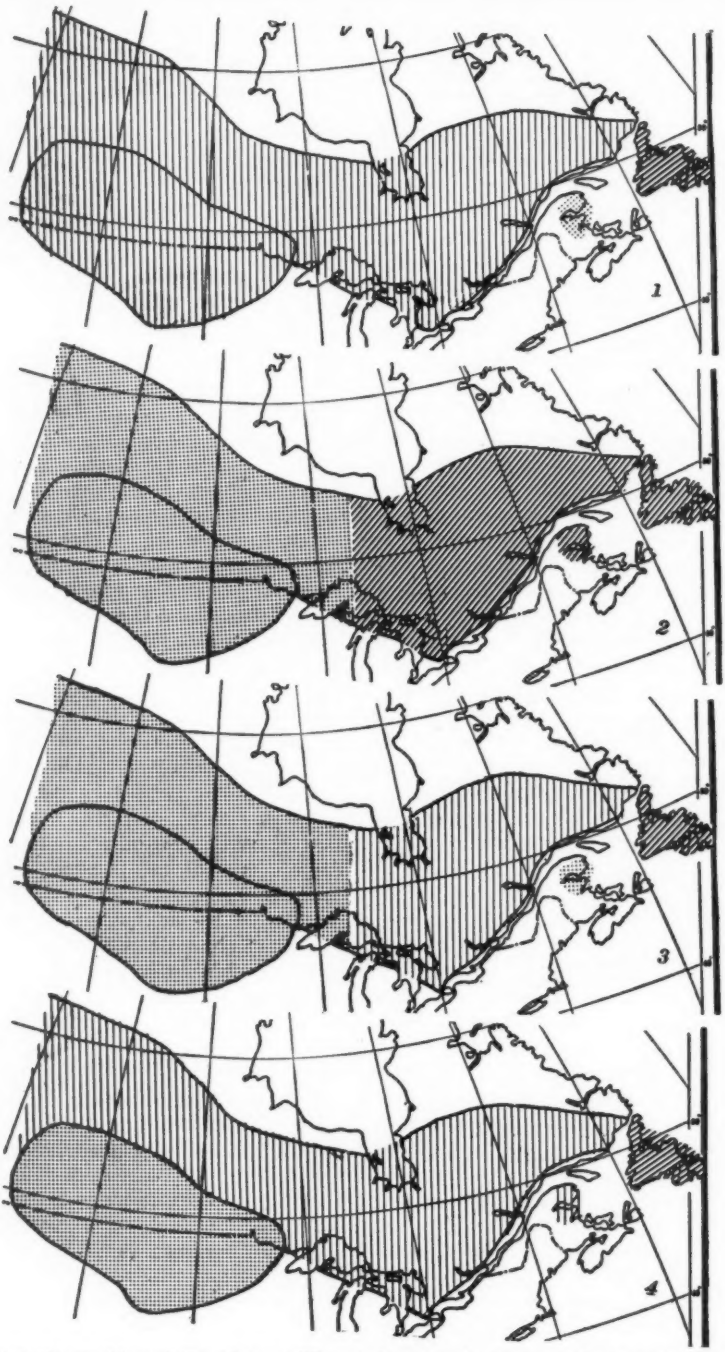
Petersen (1947) presents a study of geographical variation in sixteen species of Fennoscandian butterflies. Of these, three show no appreciable geographic variation in the characters studied, and five vary in size, or another single character only. The first species of interest here is *Pieris napi* Linnaeus (Pieridae) for which four different characters are analyzed. Petersen uses isophenes (equal value contours) to indicate geographical changes for each character separately. Figures 9-12 show the results of my plotting the isophenes of one variate superimposed upon those of another. Varying degrees of discordance are immediately evident, and it is obvious that the three described subspecies, whose type localities are indicated in the figures, could not begin to indicate the geographical variation of this species if they included any populations other than those in the immediate vicinity of the type locality. The crisscrossing of isophenes results in a multiplicity of possible character combinations. The same sort of discordance is also evident in the seven other species for which Petersen treats more than one character. These include one other pierid and six nymphalids.

Polytopic races. The phenomenon of selection of a particular single character to predominance in more than one population of a species is common in many groups of animals. Several of the characters analyzed in Brown's *Coenonympha* paper show a striking degree of polytopy (see Figs. 6 and 7). In his *Oeneis uhleri* paper, Brown (1953*a*) gives data to indicate that series from Gothic, Colorado, and the Laramie Mountains, Wyoming, are much more richly ocellate on the undersides of the wings than are intervening Colorado series from the Rampart Range and Hall Valley. A more subjective example is *Euphydryas editha* Boisduval (Nymphalidae). In this species, three very small-sized subspecies have been described from rather high altitudes. One of these is from Alberta, one from Mt. Thielsen, Oregon, and one from the Tioga Pass area in California. They are all strikingly smaller in size than surrounding populations from lower altitudes.

The females of *Papilio dardanus* Brown (Papilionidae) are highly polymorphic and usually mimetic. This species ranges over most of Africa south of the Sahara, and Ford (1936) points out that male-like females are found only in Madagascar, Grand Comoro Island, Abyssinia, and Somaliland. If we lump populations, we find that in two groups of *dardanus*, male-like females occur (i.e., these populations show little or no sexual dimorphism), while between these groups, along the coast of Kenya, Tanganyika, and Mozambique, the populations are highly polymorphic in the female. Presumably one might be justified in erecting a polytopic race that included only monomorphic populations, but this cuts across the boundaries of the described races erected on other characters, primarily in the males. In short, the existence of polytopy for a particular character does not mean that other characters are polytopic in the same geographical pattern. Such cases present the taxonomist with the choice: emphasize by nomenclatural means the polytopic characteristics, or ignore polytopic phenomena in favor of names based on other kinds of geographical variation.

Variation in Completely Isolated Populations

Continental populations. In the present state of our knowledge, we cannot with confidence estimate the degree and effectiveness of the apparent isolation thought to separate many butterfly populations occurring on continental land masses. One case in which isolation of populations is fairly well established is *Oeneis alberta* Elwes and Edwards (Satyridae). F. M. Brown (1953*b*, and *in litt.*) points out that subspecies *alberta* (Alberta and Saskatchewan) is isolated by a great distance from subspecies *oslari* Skinner from Colorado, while the latter is



FIGS. 1–8. Geographic variation of seven different characters in *Coenonympha inornata* Edwards. Junctions between different kinds of shading indicate that adjacent populations are significantly different from one another in the particular character mapped as determined by F. M. Brown (1955). The sharpness of the boundary is, of course, to a large extent a statistical artifact. The heavy black lines indicate the approximate ranges of two of the currently recognized continental subspecies, *inornata* and *benjamini* McDunnough. The characters mapped in these figures are as follows. FIG. 1. Radius of left forewing of male. FIG. 2. Frequency with which at least traces of an apical ocellar spot occur on upper side of forewing of male. FIG. 3. Frequency with which at least traces of an apical ocellar spot occur on under side of forewing of male.

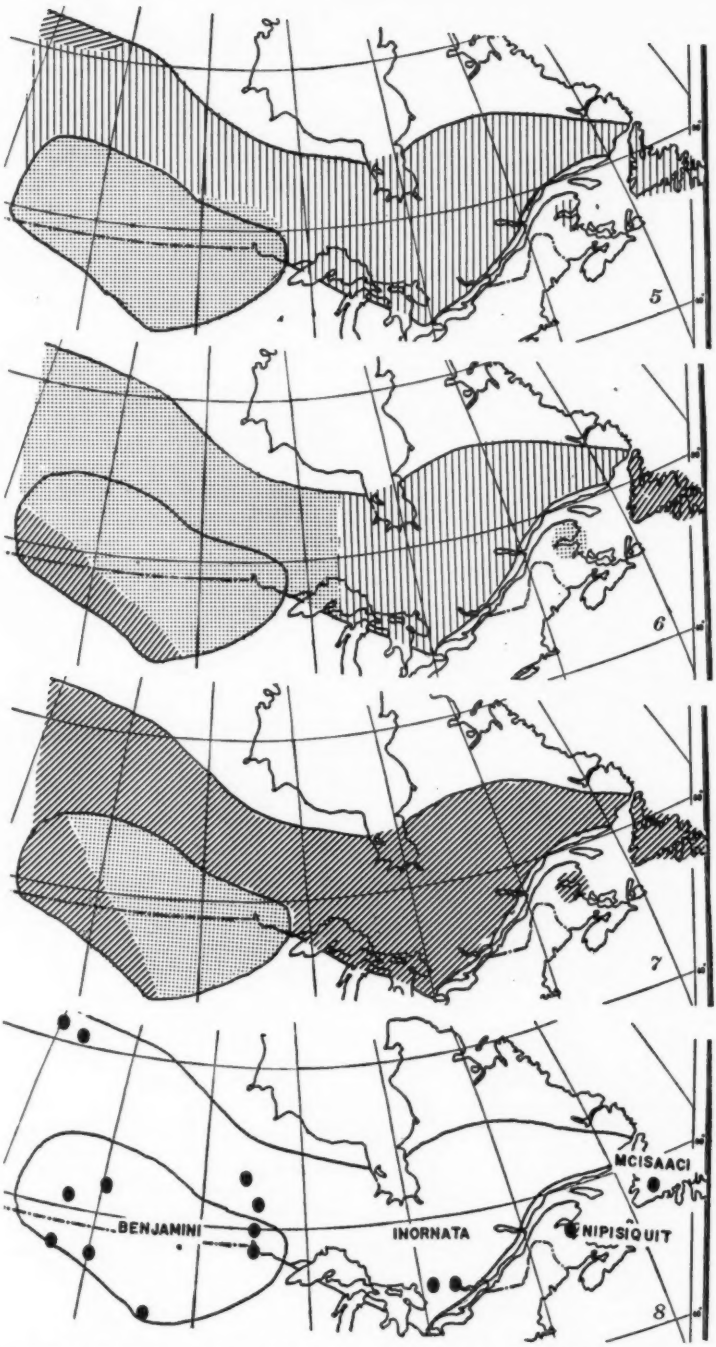
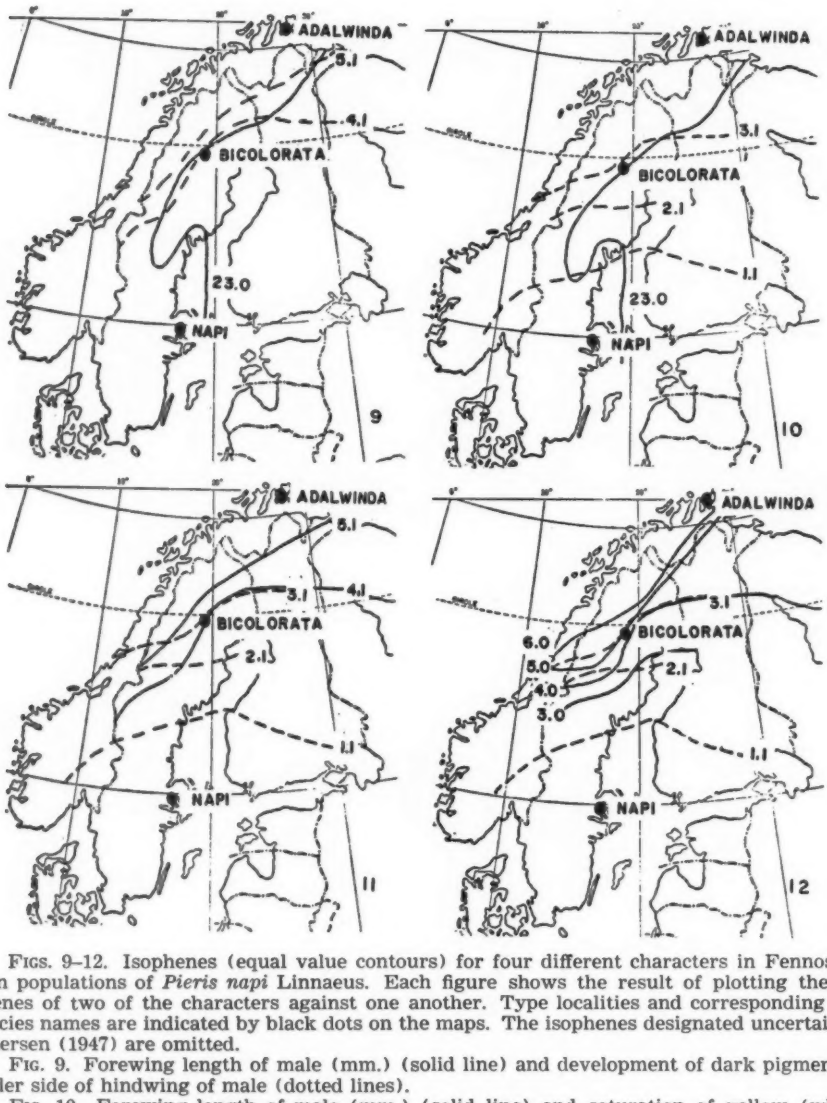


FIG. 4. Average condition of ray on under side of hindwing of male. FIG. 5. Frequency with which ocellar spots occur in submargin on under side of hindwing of male. FIG. 6. Frequency with which dark chevrons occur in submargin on under side of hindwing of male. FIG. 7. Frequency with which basal light patches occur on under side of hindwing of male. FIG. 8. Names and approximate ranges of the currently recognized subspecies. Solid circles indicate the geographical points from which statistically treated samples were obtained. The subspecies borders drawn by Brown were also based upon smaller samples which could not be treated statistically.



FIGS. 9–12. Isophenes (equal value contours) for four different characters in Fennoscandian populations of *Pieris napi* Linnaeus. Each figure shows the result of plotting the isophenes of two of the characters against one another. Type localities and corresponding subspecies names are indicated by black dots on the maps. The isophenes designated uncertain by Petersen (1947) are omitted.

FIG. 9. Forewing length of male (mm.) (solid line) and development of dark pigment on under side of hindwing of male (dotted lines).

FIG. 10. Forewing length of male (mm.) (solid line) and saturation of yellow (white) ground color on upper side of hindwing of female (dotted lines).

FIG. 11. Development of dark pigment on under side of hindwing of male (solid lines) and saturation of yellow (white) ground color on upper side of hindwing of female (dotted lines).

FIG. 12. Forewing length of male (mm.) (solid line) and degree of development of dark pigment on upper side of forewing of female outside discal and apical fields (dotted lines).

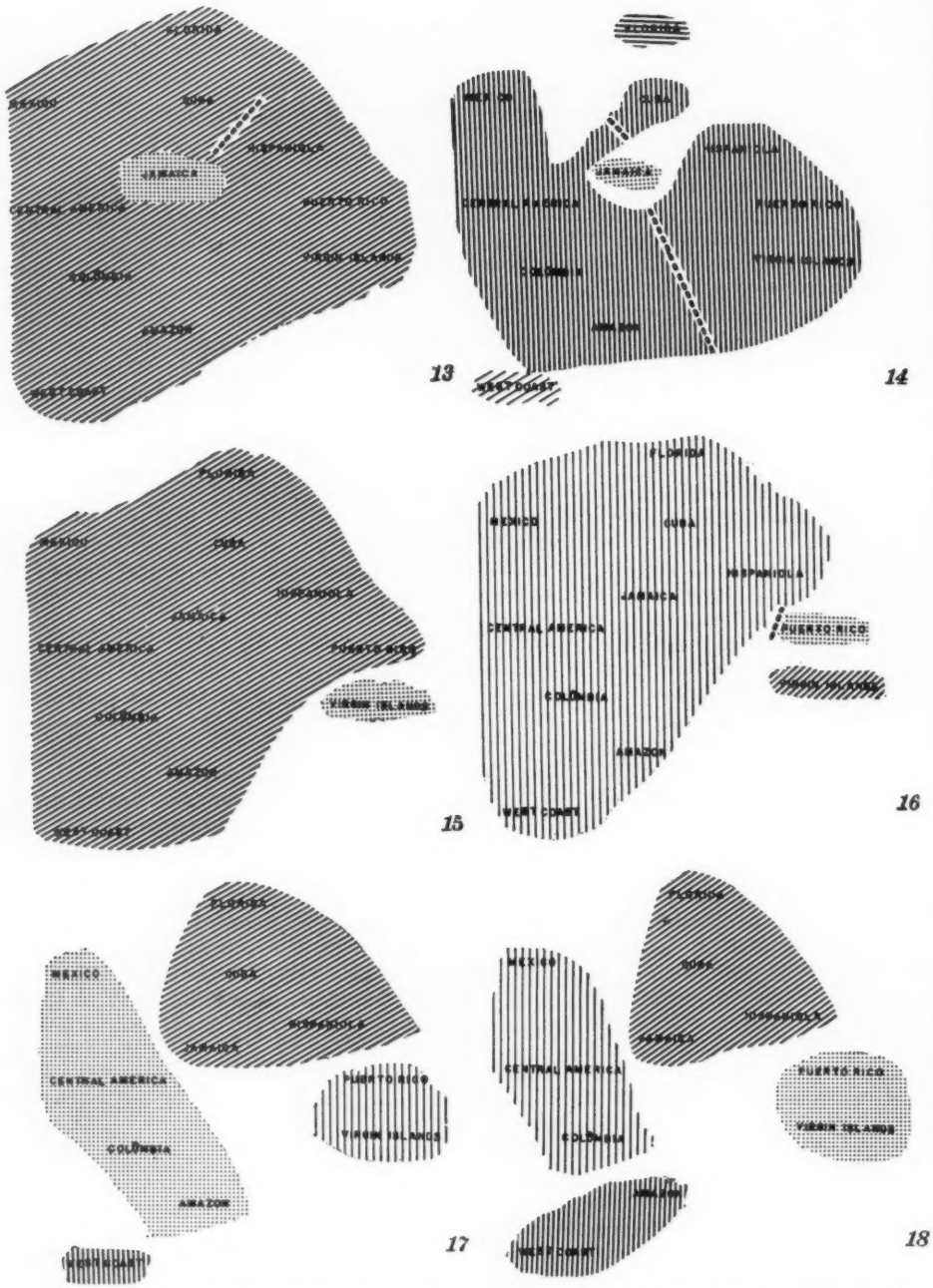
separated by hundreds of miles from *daura* Strecker which is restricted to certain parts of the White Mountains of Arizona. Brown statistically contrasts several different characters in these widely separated groups of populations. He shows that *daura* differs significantly from *oslari* in the size and color of both sexes, and also in two banding characters in the males. Two other banding characters also approach significance. Every one of the six characters in which *daura* differs significantly from *oslari* appears to be clinal when specimens of subspecies *alberta* are taken into consideration. These apparent clines are steeper, however, between Colorado and Arizona than they are between Canada and Colorado. Since breeding experiments have not been carried out, it is impossible to tell whether or not these three groups of populations have attained species level.

As mentioned at the beginning of this paper, van Son has cited *Papilio ophidicephalus* as an example of a continental species in which completely isolated groups of populations are known to exist. Some of these isolates are recognized by van Son as subspecies, since they seem to show a certain amount of character concordance and intergradation. Subspecies *chirinda* van Son ranges from the high mountain forests of eastern Southern Rhodesia to the coastal forests of Portuguese East Africa. It is separated from subspecies *entabeni* van Son of the Zoutpansberg Range in the northern Transvaal, "by a complete barrier of low veld thorn country over 100 miles wide . . ." *Transvaalensis* van Son and *ayersi* van Son are separated from *entabeni* and each other "by similar gaps." *Phalusco* Suffert ranges from the eastern Cape forests near Kingwilliamstown to the Karkloof forest of Natal. Van Son goes on to say that "any specimen of any of these subspecies can be identified without reference to the label, with an exactitude of 100%, as no intermediate specimens appear to exist in nature." Reference to Mayr, Linsley, and Usinger reveals a second, and equally valid interpretation of this data. According to their discrimination grid (p. 79) such groups of populations could equally well be interpreted as a complex of closely similar species, or *Artenkreis*. This is also true of *Oeneis alberta*, and until breeding experiments are made it will be impossible to tell whether or not these population aggregates belong to the same species, let alone to decide as to their racial status. In both cases a certain amount of character concordance is suggested. Wilson and W. L. Brown point out that in cases showing possible character concordance such as this "there is always the distinct possibility, . . . that the allopatric populations have already attained species level."

Insular populations. The only really good study of primarily insular butterfly populations known to me is the biometrical study of variation in *Heliconius charitonius* (Linnaeus) (Nymphalidae) by F. M. Brown and Comstock (1952). This species ranges from equatorial South America north through Central America to Texas. It is also found in Florida, the Greater Antilles, and some of the Lesser Antilles. The Floridian and Antillean populations are, presumably, completely isolated geographically. Figures 13-24 show the variation of a number of the characters studied by Brown and Comstock in relation to the described subspecies. The characters themselves are discussed in the captions to the figures. These figures indicate that geographical variation among the insular populations is of essentially the same discordant type as that found among continental populations of the same species. Unfortunately, I am not aware of any other study of this kind among the butterflies.

Discussion and Conclusions

The subspecies concept and its usefulness have been the topic of several critical commentaries during the last few years. The object of the growing discontent seems to be an arbitrary subspecies category that fails to describe intraspecific variation accurately. There is no need to review these papers here, but it may be



FIGS. 13–24. Geographic variation in individual characters of *Heliconius charitonius* (Linneaus) as based on the statistical analysis of Brown and Comstock (1952). Statistically significant differences are indicated by the breaks between different types of shading and by solid black lines. Noticeable differences that approach significance are indicated by dotted lines. FIG. 13. Mean wing length. FIG. 14. Indices of yellow wing bands on upper side of wings. These indices show relative widths of these bands from population to population. FIG. 15. Number of yellow spots occurring on upper side of forewing of male. FIG. 16. Number of yellow spots occurring on upper side of forewing of female. FIG. 17. Frequency of yellow spot *A* on upper side of forewing of male. FIG. 18. Frequency of yellow spot *A* on upper side of forewing of female.

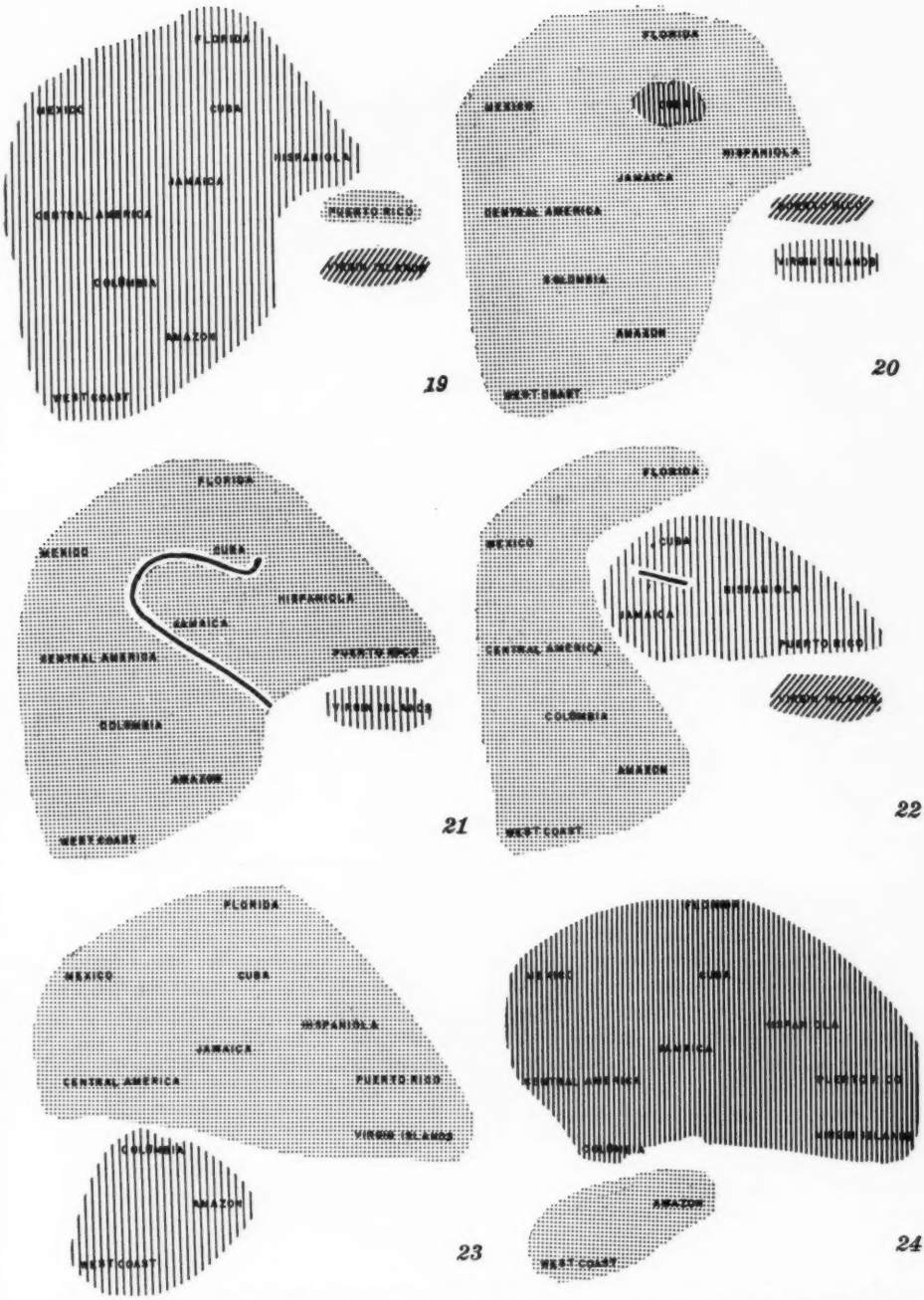


FIG. 19. Frequency of yellow spot *D* on upper side of forewing of male. FIG. 20. Frequency of yellow spot *D* on upper side of forewing of female. FIG. 21. Frequency of yellow spot *F* on upper side of forewing of male. FIG. 22. Frequency of yellow spot *F* on upper side of forewing of female. FIG. 23. Frequency with which black scales are found laving yellow bands in male. FIG. 24. Frequency with which black scales are found laving yellow bands in female.

mentioned that they express the discontent of systematists working on a number of different groups of animals.

The purpose of this survey has been to determine whether or not the subspecies category was of use in describing the geographic variation of butterflies. Most of the papers discussed were selected because they were detailed and because they described character variation independently of recognized subspecies boundaries, thus making possible a study of each individual character. I believe I have been able to cover most of the recent papers that qualify under these conditions. If any were missed, it was not through any attempt on my part to bias the examples used, but through ignorance of the literature. Therefore, this survey is in a sense a random one; its conclusions are based on a fair summary of information given in the examples studied.

The studies surveyed reveal that geographical discordance of character variation is widespread among the butterflies. Concordance does not necessarily increase with degree of geographic isolation, though the small size and local nature of some insular samples may create an initial impression of lessened discordance. The concordance claimed for some completely allopatric populations may be a sign that these have reached species level, a possibility clearly not ruled out by the existing data. Arbitrary boundaries drawn to separate continental subspecies may agree with a single character shift, or with none; rarely does such a boundary mark the apparent concordant change of two or more characters over more than a short distance.

In view of the prevailing discordance of geographical patterns followed by different variates, racial partition of butterfly species is not only arbitrary, but it must also necessarily weight some variates and ignore others, without regard for the biological significance of any of them. The best that can be hoped for now is an analysis of variation by individual characters, avoiding arbitrary subdivision of the species. Such analysis will eventually yield a less distorted picture of species formation than that to which the artificial subspecies now inevitably leads.

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This paper was prepared by **NICHOLAS W. GILLHAM**, while a graduate student at the Biological Laboratories, Harvard University. He would like to express his appreciation to F. M. Brown, W. L. Brown, Jr., P. J. Darlington, Jr., R. B. Willey and F. H. Rindge, for offering critical and helpful suggestions which greatly aided in the preparation of this paper.

On the Evolution and Systematics of Ciliated Protozoa

JOHN O. CORLISS

Part II

Order 7. APOSTOMATIDA Chatton and Lwoff, 1928

A highly specialized and modified group, comprising only some three dozen species, whose unity was not recognized at all prior to the exhaustive investigations of Chatton and Lwoff. Now the order is universally accepted as having independent status among the holotrichs, but its evolutionary history and its exact relationship to other orders remain obscure.

The majority of apostome species occur in or on marine Crustacea, undergo a polymorphic life cycle, often involving two hosts, possess fewer than twenty-two rows of somatic ciliature, arranged in the mature stage in dextral spirals, and characteristically have a small ventrally-placed cytostome surrounded by a unique structure known as the rosette (see Pl. III, Fig. 5). A small field of thigmotactic ciliature in the vicinity of the mouth, not truly buccal ciliature although it has been called that in the literature, plays an important role in the morphogenetics of fission and stomatogenesis (see esp. Chatton and Lwoff, 1935, their culminating monograph on the group).

A very small group of ciliates included in the order do not show the rosette so typical of the majority. The species *Cyrtocaryum halosydnae* is an important representative of this group (Fauré-Fremiet and Mugard, 1949*b*). This organism, whose host is a marine polychaete, must be assigned to the APOSTOMATIDA on the basis of its pattern of infraciliature and the morphogenetics of its life cycle, in spite of its lack of both mouth and rosette and its association with an annelid.

The complexities of stomatogenesis and fission in the ontogeny of the apostomes suggest to the writer an evolutionary origin above the gymnostome-trichostome level. It seems possible that the orders in closest phylogenetic relationship with this small, quite highly evolved group are the hymenostomes and/or the thigmotrichs.

The return to the ancestral type of bipolar ciliature, seen in the process of binary fission here as well as in neighboring holotrichous orders, may be considered as an indication, once again, of the recapitulative picture of phylogeny in ontogenetical development of such otherwise complex-appearing forms.

Representative genera include *Foettingeria, Gymnodinioides, Ophiuraespira* (Pl. III, Fig. 5), and *Spirophrya.*

Order 8. THIGMOTRICHIDA Chatton and Lwoff, 1922

Another entire order of holotrichous ciliates established through the monographic works of Chatton and Lwoff (1949, 1950; and preliminary papers cited therein). The taxonomic contributions of many others, including in more recent years such prolific investigators as Kidder and Kozloff in America and Z. Raabe (1949, 1950; and earlier) in Poland, likewise have been invaluable in gaining an understanding of relationships within this curious group of symbiotic ciliates. The anteriorly located thigmotactic area, anatomically and physiologically differentiated, gives the order its name and is characteristic of all species included here, although it is not an exclusive feature of this holotrichous order alone.

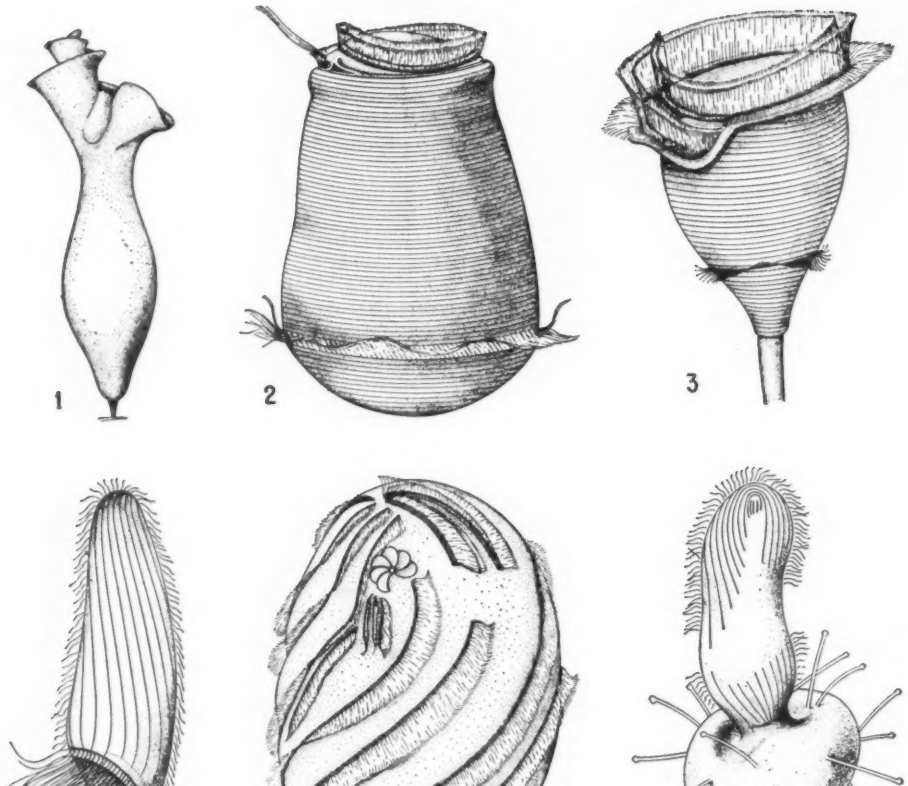


PLATE III. Representative members of the holotrichous orders CHONOTRICHIDA, PERITRICHIDA, THIGMOTRICHIDA, APOSTOMATIDA, and SUCTORIDA. FIG. 1. *Spirochona*, a typical chonotrich. Note anterior spiralling of the body, giving the order its name; apical end of the organism actually represents its ventral surface. Note stalk, not produced by a scopula in this order, and lack of ciliation over the general body surface of the mature form shown here. The infraciliature of the larval form reveals its holotrichous affinities. (Redrawn mostly from Guilcher, 1951.) FIG. 2. *Telotrochidium*, a motile member of the sessiline peritrichs, perhaps permanently in a telotroch (larval) stage. Note the peristomial ciliature, with its counterclockwise winding, and the aborally located locomotor fringe. (Redrawn from Fauré-Fremiet, 1924; and Lynch and Noble, 1931.) FIG. 3. *Vorticella*, a widely known sessile peritrich. Note the stalk (only very small portion shown), secreted by an organelle of ciliary origin known as the scopula, the sinistral winding of the peristomial ciliature, and the inconspicuous locomotor fringe often not in evidence externally at all in this attached stage of the organism. (Redrawn from Noland and Finley, 1931.) FIG. 4. *Boveria*, a typical episymbiotic thigmotrich. Note position of the buccal apparatus: completely at the posterior pole. Area of thigmotactic ciliature, located near the anterior pole and poorly developed in this genus, is not visible here. (Redrawn from Pickard, 1927.) FIG. 5. *Ophiuraespira*, a representative apostome. Note the curious rosette, a unique structure, in the oral area and the spiralling of ciliary rows in the mature feeding stage, shown here. The simple symmetry of ancestral ciliates is revealed in other stages of the life cycle not depicted here. (Redrawn from Chatton and Lwoff, 1935.) FIG. 6. *Discophrya* (=*Podophrya* ?), a representative simple suctorian, showing the last stage in the phenomenon of endogenous budding. Note presence of cilia on the emerging larval form and its absence on the tentacle-bearing body of the mature, parental form; both, however, possess an infraciliature (*cf.* Pl. I, Fig. 3). Stalk of the attached stage is secreted by a scopula, as in peritrichs. (Redrawn from Guilcher, 1951.)

Fauré-Fremiet (1950*a*) was the first to offer an interpretation of thigmotrichs, buccal organelles, and of their fate in ontogeny, which can be considered of great phylogenetic significance. This principally involved only a relabelling of the parts of the oral apparatus, so precisely described by Chatton and Lwoff, making it possible to realize that a fundamentally tetrahymenal arrangement of mouth structures exists here. Fauré-Fremiet's hypothesis thus allows one to believe that the HYMENOSTOMATIDA is the immediate ancestral group for the THIGMOTRICHIDA. In the well-established family Hemispeiridae, for example, the genus *Ancistrum* is strikingly similar to certain of the Pleuronematina hymenostomes. At the same time the evolutionary transition, within that thigmotrichous family, from *Ancistrum* through genera like *Proboveria* and *Boveria* to *Hemispeira,* in which the buccal apparatus is located entirely at the posterior pole, is beautifully evident (Chatton and Lwoff, 1936; Chatton, 1936).

The writer suggests gracing each of the two "tribes" of Chatton and Lwoff with the elevated title of suborder, continuing to credit these workers with the slightly emended names.

Suborder (1) Stomatina Chatton and Lwoff, 1939

Composed of species with sub-equatorially to terminally located cytostomes. As mentioned above, the buccal apparatus may be homologized completely with the tetrahymenal organization of the HYMENOSTOMATIDA, especially as found in the Pleuronematina where its posterior poleward migration and its autonomization in stomatogenesis are already in evidence.

Descriptive details of the morphogenetics of fission and new mouth formation, although essential for full comprehension of the evolutionary relationships proposed, are for this order, as well as for the preceding and following ones, beyond the scope of the present paper. The reader must be referred to Chatton and Lwoff (1949) and Fauré-Fremiet (1950*a*).

Representative genera include *Thigmophrya, Conchophthirius, Ancistrum, Boveria,* and *Hemispeira;* a species of *Boveria* is depicted in Plate III, Figure 4.

Suborder (2) Rhynchodina Chatton and Lwoff, 1939

Composed of thigmotactic holotrichs characterized by the functional replacement of the cytostome by a sucker. This unique organelle, sometimes occurring at the distal end of a tentacle, is located anteriorly in the vicinity of the thigmotactic ciliature; only a vestige of buccal ciliature is retained. Chatton and Lwoff (1949) have offered a detailed description of the genesis and development of the sucker, a specialized ciliary derivative. Guilcher (1951) believes no homology exists between this rhynchodinid organelle and the suctorian tentacle.

The mode of fission, even in such seemingly aberrant forms as *Sphenophrya,* in which the ciliature in most species of the genus is represented in the mature form only by its infraciliary counterpart, and in which a budding process not unlike that seen in other holotrichous orders occurs, is still fundamentally homothetigenic and perkinetal in nature.

Representative genera include *Ancistrocoma, Hypocomella,* and *Hypocoma.*

Order 9. PERITRICHIDA Stein, 1859

A long-known group of ciliates embracing nearly one thousand described species, thus the largest of all ciliophoran orders. The peritrichs, in spite of distinctive features, may be considered fundamentally holotrichous, principally on the basis of a modern intrepretation of the composition of their oral ciliature. Many of their apparent differences, including shifts in anatomical axes, appear to be related to the fact that the majority of them long ago adopted the sessile habit; but the scopula, which secretes the peduncle or stalk, is very likely a homologue of the

ciliary thigmotactic area present in other orders of holotrichs (Fauré-Fremiet, 1905, 1910). The immature stage of stalked forms, in reality a larval form although it is produced by a type of binary fission not identical with budding, is known as the telotroch or swarmer; it is an active swimmer and its migration away from the mature parental form serves the all-important function of dispersal.

The "key" characters which are typically employed to separate the peritrichs from all other ciliates are the very ones which may now be used to justify their affiliation with the subclass Holotricha: conventionally the very presence of a conspicuously developed adoral wreath of ciliary organelles at the unattached end of the sessile forms has excluded this order from the holotrichs; and its counterclockwise winding, toward the cytostome, has prevented its inclusion among the spirotrichs (see Pl. III, Figs. 2 and 3, and contrast with other figures in Pls. II, III, IV). But if one postulates the group's origin from the HYMENOSTOMATIDA-THIGMOTRICHIDA line, then reinterpretation can cause both of the characteristics of the peritrichous oral ciliature just mentioned to lose their uniqueness.

The Furgason-Fauré-Fremiet hypothesis insists upon recognition of at least a primitive AZM among the holotrichs, for example, in the hymenostomes and thigmotrichs, as discussed in preceding sections. Among the simpler hymenostomes it can be seen, particularly in the excellent figures of Mugard (1949), that both dextral and sinistral winding of the three membranelles of the AZM may be said to exist. The arrangement can be considered as clockwise in genera like *Uronema, Porpostoma,* and possibly *Tetrahymena;* but it is definitely counterclockwise in related forms such as *Anophrys* and *Lemboides* (=*Paralembus*), in which the AZM secondarily has been thrown over to the right. Among the Tetrahymenina hymenostomes themselves, then, the direction of winding would seem to be of no major taxonomic importance. In the Stomatina of the THIGMOTRICHIDA, where the AZM-homologue has been displaced to the right without exception, the spiralling is always counter-clockwise, viewed from the oral pole and coursing toward the cytostome. Now in all the PERITRICHIDA, for example, *Vorticella* and *Trichodina,* the winding again is counterclockwise if viewed in the same manner. In many thigmotrichs the oral apparatus has migrated onto the posterior pole; by homology, the "upper" pole of the stalked peritrichs, then, is phylogenetically the posterior pole. The only difference in the winding, between thigmotrichs and peritrichs, is this: the helicoidal path in the first group is "downstairs" with respect to the path toward the mouth from the distal end of the buccal ciliature; it is "upstairs" in the second group.[9] This fact influenced Chatton (1936, 1938) to maintain vigorously that the oral ciliature could not be homologized in the two groups, in answer to Fauré-Fremiet's earlier suggestions (1905, 1910, 1924) of a close evolutionary relationship between certain thigmotrichs and the vorticellid peritrichs.

A look at the infraciliary picture, now

[9] As one can conveniently demonstrate with several wire pipe cleaners, the spiral of the thigmotrichs, physically speaking, is actually dextral in nature and that of the peritrichs, sinistral. But if one designates with a mark the "cytostomal" end of the wire in each case, it becomes apparent that the dextral spiral leads away from the mouth and the sinistral, toward it. By simply shifting the plane of the mouth a sufficient distance (with respect to the "distal end" of the wire), either system can be transformed into the other. In the evolution of the peritrichs from the thigmotrichs it is not unreasonable to suppose that somatic morphogenetic movements could, without difficulty, account for the anatomical change in the plane or level of the cytostome proper.

Problems arising over use of the words "dextral" and "sinistral," with regard to the winding of the ciliate AZM, have been discussed in considerable detail by Delage and Hérouard (1896, pp. 454–456) and will receive more attention from the writer in a later separate paper.

more generally possible, may cast some light on the difficult problem. Externally the peristomial ciliature of peritrichs is composed of two or three wreaths or circlets of so-called semi-membranes, one outer and one or two inner, depending upon the species. Quite apart from the postulated phylogenetic evidence of homology, the actual cytological picture of the bases of these ciliary structures strongly suggests an historical identity of parts in all three groups: hymenostomes, thigmotrichs, peritrichs.

Without going into details, this appears to be the picture which can now be pieced together regarding the outer membrane of the peritrichous oral apparatus: it is more delicate than, and separated from (to the right of), the others (Noland and Finley, 1931); its base is composed of probably only a single row of basal granules or kinetosomes (Chatton and Villeneuve, 1937; Uzmann and Stickney, 1954); near its proximal end, before descent toward the cytosome, it shows an area of argentophilic "bars," "rods," or "striae" (observed by the writer, unpublished; also figured by Chatton and Villeneuve, and by Uzmann and Stickney); and its descending portion is fused into a typical right-hand undulating membrane (Noland and Finley; Uzmann and Stickney). The writer believes very strongly that this entire outer membrane may be considered the UM (undulating membrane) of the peritrichs—all its features are identical with those of the well-established UM of many other groups representing both holotrichous and spirotrichous orders.

By similar reasoning based upon similar data, the inner one or two ciliary wreaths of the apical crown may be postulated to be the true AZM of the PERITRICHIDA, homologous with the AZM of the tetrahymenal hymenostomes. Its extensive development does not necessarily militate against this. And its conceivably end-to-end fusion of primitively separate membranelles, perhaps with subsequent lateral duplication in forms with two rings of such ciliature today, its counterclockwise winding, its shift in position related to eversion of most of the original buccal cavity into an expanded peristomial field—these may also be considered as having arisen secondarily. Space does not permit further defense of these postulations. But if such transformations have truly happened as intimated, then they should not be allowed to interfere with recognition of more fundamentally important factors when attempting to trace the evolutionary history of the group. With regard to the infraciliary bases of the membranelles, seen to be of a multiple kinetosomal nature in silver preparations, it is quite interesting to note that Schröder (1906) half a century ago reported three rows of granules at the base of each "inner membrane" in a species of *Vorticella*. Other more recent workers have also noted the composite nature of the membranelles with techniques not including silver impregnation.

With recognition of a holotrichous AZM and UM, derived fundamentally from the tetrahymenal type, and with acceptance of the probability that thigmotrichs, with their more and more posteriorly located buccal apparatus, arose from hymenostome-like ciliates, it does not appear too unreasonable to believe that the peritrichs, with similar localization of oral ciliature and thigmotactic (scopula) area, arose from thigmotrichous forms. In spite of their having enjoyed a long subsequent evolutionary history of their own, the inclusion of the PERITRICHIDA in the subclass Holotricha, tentatively, at least, seems justifiable.

Two even more puzzling features of peritrichs still require mention: the posterior circlet of locomotor ciliature of such importance to the telotroch; and the polarity of the body with respect to binary fission. In both instances modern research on the problems involved is conspicuous by its absence.

Unlike the ringed ciliature of certain suctorian larvae, the locomotor fringe of the telotrochs of the present order forms

a complete and closed ring; furthermore, its infraciliature is complex in comparison (Klein, 1928; Kofoid and Rosenberg, 1940; Fauré-Fremiet, 1950*d*; and others). Plates of basal granules bear partly fused, semimembranous ciliature, with an orientation of the kinetosomal elements, five to six in a row, which forms an oblique angle with the longitudinal axis of the body. The origin and history of this curious band still defies elucidation, and no hypothesis has been conceived regarding it which does not conflict with data relative to other peritrichous features.

The problem of polarity and axial homologies is equally vexing. Morphological, physiological, locomotor, and phylogenetic axes may nearly all be different from one another here! For example, the oral surface has been considered anterior, posterior, or ventral; the stalk (in sessile forms), posterior, anterior, or dorsal. Telotrochs typically swim with aboral pole directed forward. The apparent plane of division (is it primarily or secondarily longitudinal?) only serves to complicate the problem. If the separating filial organisms during binary fission are not mirror images of one another—and precise data concerning this important point seem to be entirely absent from the literature—then a modified homothetigenic division probably is taking place. Stomatogenesis (Chatton and Villeneuve, 1937) has become completely autonomous in this order, another evidence of its high degree of specialization and differentiation and of no help at all in determining axial relationships.

The division of the order here is that suggested by Kahl (1930–1935):

Suborder (1) Sessilina Kahl, 1935

Composed typically of stalked forms, solitary or colonial, some leading an episymbiotic existence. The buccal ciliature has been discussed above; the somatic ciliature is limited to the enigmatic locomotor fringe which encircles the body near the adoral pole. Although Chatton (1936) insisted on the existence of an extensive somatic infraciliature arranged concentrically over the body in such a way that the rule of desmodexy is not contradicted, it is possible that surface sculpturing or ectoplasmic-pellicular pores of some sort—argentophilic structures which have been described by a number of investigators—might have been mistaken for kinetosomes by Chatton.

The migratory form in the life cycle, the telotroch, may be produced by a binary fission, often of a very unequal nature, or may arise by total transformation of the mature form into a swimmer, with appearance of the locomotor fringe and abandonment of the stalk. There are many minor variations. Species of at least one genus, *Telotrochidium*, appear to be permanent telotrochs, with fission, etc., taking place in that stage: the scopula seems to have lost its stalk-producing ability and the locomotor fringe is indefinitely retained (see Pl. III, Fig. 2).

Conjugation typically involves so-called macro- and micro-conjugants, with total fusion of the two members of the pair in some species. Such a "syngamous" type of conjugation is known among other groups of ciliates as well, including the holotrichous orders CHONOTRICHIDA and SUCTORIDA.

Although hundreds of species have been described in this suborder, very little morphogenetic work of a type helpful in high level comparative systematics has been published to date. Of many representative genera, *Vorticella* (Pl. III, Fig. 3), *Epistylis*, and *Zoothamnium* may be cited.

Suborder (2) Mobilina Kahl, 1935

The typically unattached species, with free-swimming forms in all stages of the life cycle. Some groups within this suborder have a recognizable separate telotroch stage, and some have been considered to be, phylogenetically speaking, nothing more than highly specialized, permanent telotrochs themselves. The "oral-aboral" axis, in contrast to that shown by members of the preceding suborder, may be greatly shortened. The development of a basal or adhesive disk,

often equipped with a complex of ribs, myonemes, and a skeletal or denticulate ring, is a further specialization found in many of these forms.

The buccal ciliature is essentially identical with that of the preceding suborder. The somatic ciliature, except for the ciliary girdle, is again commonly absent.

A representative genus is *Trichodina*, some of whose many species exhibit a truly parasitic mode of life in or on a variety of aquatic animals. *Urceolaria* also should be mentioned here.

Raabe (1952) has recently described a species considered by him to be intermediate between the two suborders. Such cases serve to emphasize the inadvisability of dogmatic insistence upon the existence of clear-cut lines between closely related groups of genera or species.

Subclass 2. Spirotricha Bütschli, 1889

Although the spirotrichous ciliates exhibit considerable variation in form and structure, the great diversity in fundamental features which is so prevalent among the holotrichs appears to be absent here. Their morphology is dominated by the buccal ciliature composing the adoral zone of membranelles, the prominence of which is accentuated by an increasing loss of simple somatic ciliature. In the most highly evolved order here, in fact, simple cilia are replaced entirely by the compound ciliary organelles known as cirri.

The AZM, as in the highly specialized peritrichous holotrichs treated above, may be considered as having been derived from the inconspicuous buccal ciliature of the lower HYMENOSTOMATIDA, but the evolutionary path appears to have been more direct in the present case. Among the spirotrichs the AZM typically appears as a prominent, extensively developed, but fundamentally very uniformly composed, ciliary structure lying along the left-hand side of the general peristomial or buccal-cavity area[10] and invariably circling clockwise (dextral spiral) from distal end toward the cytostome. Hypothetically to arrive at this condition from the tetrahymenal prototype of the hymenostomes, one need only envision, as Furgason (1940) and Fauré-Fremiet (1950*a*) have done, an increase in number, size, and extent of the component parts of the AZM. The bases of the membranelles, as seen in existing species in both groups in silver impregnation preparations, are very similar and the suggested homology does not appear to strain the evidence available. It is true that we do not have a series of extant intermediate forms, but missing links are consistently rare when and where the systematic zoologist needs them! The hymenostome genus *Porpostoma*, as mentioned above (page 86), exhibits an elongate, multiple-membered AZM and, indeed, has been classified as a spirotrich (HETEROTRICHIDA) by some workers in the past (see Mugard, 1949); but consideration of *Porpostoma* itself as the bridge across the gap may not be justifiable.

The spirotrichs appear to represent a more compact group than the holotrichs; the number of described species is much smaller, too, being less than 20 percent of the entire subphylum total if one excludes the very numerous pelagic tintinnids from the calculation. Thus the following orders will require less discussion from the point of view of phylogeny and comparative evolution.

Order 1. HETEROTRICHIDA Stein, 1859

The largest group of spirotrichs, exclusive of the TINTINNIDA, with considerable diversity exhibited among its numerous known genera. The peristomial field,

[10] The writer considers the terms "buccal" and "peristomial," and "buccal cavity" and "peristome" as well, to be fundamentally synonymous. In groups such as the peritrichs, heterotrichs, hypotrichs, and others, in which the buccal cavity secondarily has in large measure become flattened out, or even everted, and is much more extensive in area, it seems sensibly appropriate to retain the firmly entrenched and very apt terminology "peristome" and "peristomial," as long as the phylogenetic homologies are not disregarded or forgotten (see footnote 5).

homologue of the hymenostome buccal cavity (see footnote 10), has become very extensive in some species, even being drawn out into two great wings in the members of the curious folliculinid group. Often the AZM takes a turn wholly or partially around the apical end of the body before continuing its clockwise swing down along the left-hand side of the peristomial area toward the cytostome. The undulating membrane, typically where it belongs, on the right, may be very inconspicuous; in fact, it is entirely absent in a number of species.

The lability of the HETEROTRICHIDA, making it the "GYMNOSTOMATIDA" or, perhaps better, the "HYMENOSTOMATIDA," as it were, of the subclass Spirotricha, may be seen in its frequent possession of uniform ("holotrichous") somatic ciliation and in its general lack of such specialized structures as cirri. It also exhibits plasticity in its modes of stomatogenesis and in the morphogenetics of fission in general (see the monograph of Villeneuve-Brachon, 1940). Interestingly enough, the patterns of stomatogenesis are identical in various groups of the heterotrichs and the hymenostomes, ranging from the simple type involving a single stomatogenous meridian to an allegedly entirely autonomous type.

A number of heterotrichs are large, of common occurrence, and very suitable as experimental material. In the new surge of interest in application of both techniques and hypotheses of the experimental embryologist to ciliated protozoa, such forms as *Stentor* and *Blepharisma* have been popular with morphogeneticists (see Tartar, 1953, 1954; and references to works of P. B. Weisz and others in Weisz, 1954).

As mentioned briefly earlier in this paper, the family Balantidiidae, probably the most popularly known group of "heterotrichs" among parasitologists, must be transferred to the holotrichous order TRICHOSTOMATIDA on the basis of the recent precise reinvestigation by Fauré-Fremiet (1955). In this work it was shown that no true AZM exists in species of *Balantidium* and that fission and stomatogenesis are of a primitive holotrichous type.

The Licnophoridae, according to the thorough works of Balamuth (1940, 1941) and Villeneuve-Brachon (1940), properly represent a heterotrichous family although some of its species have been classified in various orders in the past. It is conceivable that on the basis of the long and independent evolutionary history of the genus *Licnophora*, as shown in its development of several rather novel structures, a separate subordinal position should be created for it within the HETEROTRICHIDA. Further study of these unusual ciliates, marine ectocommensals for the most part, may support this suggestion. Some very interesting investigations on the morphogenetics of regeneration have been carried out in the past (see Balamuth, 1940).

There are about a dozen families in this large order; among the better known genera, which might serve to represent the order, may be mentioned the following: *Condylostoma, Spirostomum, Stentor,* and *Climacostomum* (Pl. IV, Fig. 1).

Order 2. OLIGOTRICHIDA Bütschli, 1887

A specialized group of spirotrichs comprising fewer than one hundred known species, all characterized by the great reduction or complete absence of somatic ciliature. Bristles or cirri of some sort, sparsely arranged, encircle the body of a number of species. The strongly developed AZM can function in locomotion as well as in feeding (see Pl. IV, Fig. 2).

Stomatogenesis is of an autonomous type here (Fauré-Fremiet, 1953*b*). In *Halteria* the *anlage* of the new buccal ciliature occurs near the surface of the body, presumably in contact with the parental apparatus. In oligotrichs of the *Strombidium* type, however, it occurs in a sort of intracytoplasmic vacuole, not unlike the situation reported for certain

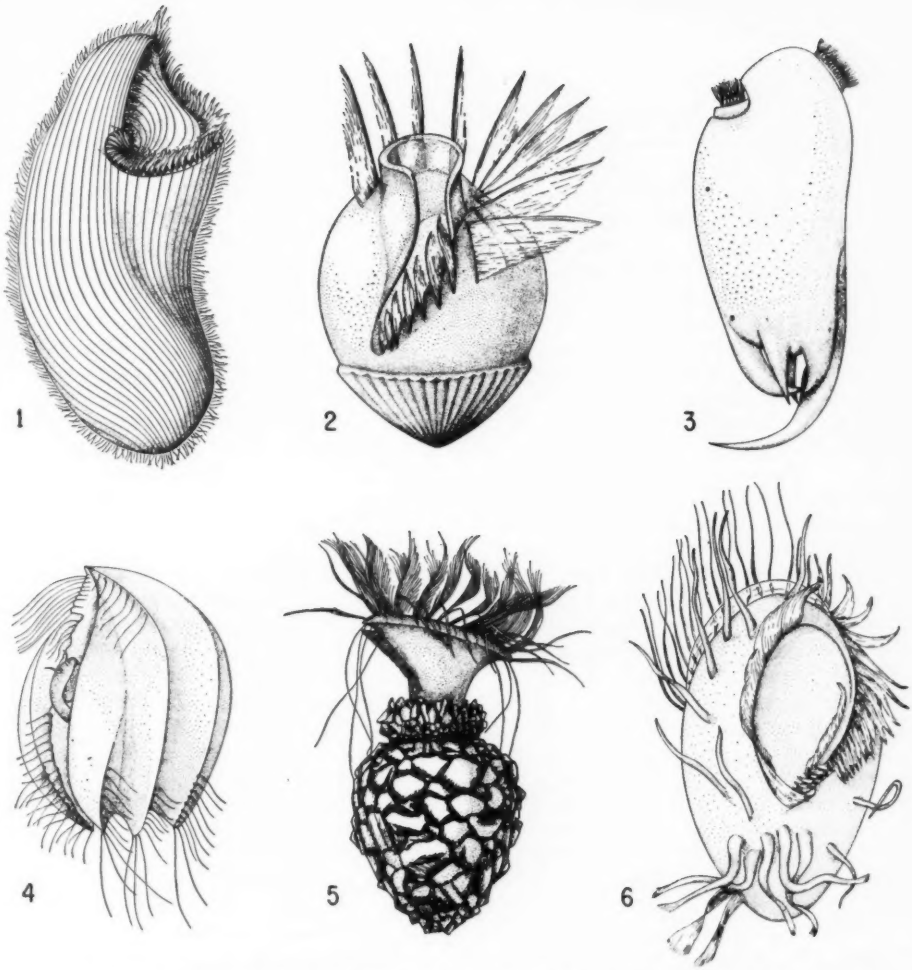


PLATE IV. Representative members of the spirotrichous orders HETEROTRICHIDA, OLIGOTRICHIDA, ENTODINIOMORPHIDA, CTENOSTOMATIDA, TINTINNIDA, and HYPOTRICHIDA. FIG. 1. *Climacostomum,* a representative heterotrich but possessor of both the holotrichous pattern of somatic ciliature and the prominently developed AZM, dextrally wound, so characteristic of all spirotrichous groups. (Redrawn from Fauré-Fremiet, 1948*a*.) FIG. 2. *Strombidium,* a typical oligotrich. Note complete lack of somatic ciliature but high development of the AZM, which encircles the apical end of the organism conspicuously. (Redrawn from Fauré-Fremiet, 1924.) FIG. 3. *Epidinium,* a representative ophryoscolecid of the order of entodiniomorphids. Note the AZM on the observer's right and a *dorsal* zone of membranelles, at a slightly lower level, on the left. Otherwise, any ciliature is conspicuous by its absence, but a somatic as well as buccal infraciliature does exist (see text). The pellicle is very firm and drawn out into spines posteriorly, a matter of value in taxonomic keys at subgeneric levels. (Redrawn from Kofoid and Christenson, 1934.) FIG. 4. *Epalxis,* a common ctenostome. Note the laterally compressed body, the sparseness of somatic ciliature, and the rigid, ribbed pellicle. The inconspicuous AZM is entirely hidden from sight in the view shown here. (Redrawn from Kahl, 1926.) FIG. 5. *Tintinnopsis,* a representative member of the huge but highly specialized pelagic order of tintinnids. Note several characteristic features, in particular the conspicuous, precisely formed lorica. Structure of the lorica is very important for taxonomy within the order but of little use in phylogenetic considerations. (Redrawn from Fauré-Fremiet, 1924.) FIG. 6. *Diophrys,* a good example of the hypotrichs, the order which presumably represents the pinnacle of pellicular differentiation in ciliate evolution. Note the broad peristomial area, the conspicuous and extended AZM, the right-hand UM, and the array of prominent cirri set in groups on the underside of this rigid-inform, dorsoventrally flattened organism. (Redrawn from Fauré-Fremiet, 1948*a*.)

species of other highly evolved spirotrichous orders (see below).

The mode of fission has very recently been exposed by Fauré-Fremiet (1953*b*) as representing a type of "inverted homothety." The two potential filial organisms, as division begins, are in such a position that their polarities are just reversed; yet the *proter* and *opisthe* are not mirror images of one another. Fauré-Fremiet terms this unique type of fission "enantiotropic" as contrasted with the much more common "homiotropic" type. Before final separation occurs, morphogenetic movements establish a juxtaposition of the filial organisms which restores an homothety more nearly of a homiotropic nature. The plane of fission actually forms an oblique angle with the axis of the initial parental body. (There are holotrichous orders, also, in which superficially oblique fission occurs among certain species.)

The postulated origin of the OLIGOTRICHIDA from the HETEROTRICHIDA seems not unreasonable and apparently has never been considered a controversial matter. There is disagreement concerning the extent of the order itself. Not entirely in agreement with Fauré-Fremiet (1950*a*, 1953*b*), the writer follows Hall (1953) and others in considering that the oligotrichs *sensu stricto* do not include the tintinnids and ophryoscolecids, which are thus treated below as separate orders.

Representative forms should include the widely distributed *Halteria* and also the genera *Strombidium* (Pl. IV, Fig. 2) and *Strombilidium*.

Order 3. TINTINNIDA Kofoid and Campbell, 1929

A most curious group of highly evolved ciliates, primarily pelagic forms, whose systematics within the order is dominated by structural features of the lorica. Nearly nine hundred species have been described through the year 1952.

The AZM is prominent and of a typical spirotrichous nature; somatic ciliature is sparse or absent. A unique structure, the so-called tentaculoid, of unknown origin and function, commonly occurs among the membranelles.

Morphogenetics of fission and of new mouth formation has not been studied precisely with modern techniques. However, the investigations of such men as Fauré-Fremiet (1908, 1924) and Campbell (1926) have shown quite clearly that in stomatogenesis the new buccal apparatus develops within an intracytoplasmic vacuole, mentioned as also characteristic of a number of oligotrichous species, above.

Kofoid (1930) has discussed factors pertaining to the evolution of forms within the order. The lorica, most useful in differentiation of genera and species, serving as a prime "key" character, is, of course, of no aid in postulating phylogenetic relationships between the tintinnids and other spirotrichous groups. Their position near the OLIGOTRICHIDA, however, will probably continue to go undisputed.

The realization in relatively recent years (see Campbell, 1954) that recognizable tintinnids (identifiable by the calcitic replacements of their loricae) exist as fossils of the Upper Jurassic has been of some paleontological importance (e.g., in stratigraphic problems) and is mentioned here, in passing, because such forms represent the only certain fossils among the Ciliophora known to protozoologists to date.

The genera *Tintinnus* and *Tintinnopsis* (Pl. IV, Fig. 5) may serve as representative of the order.

Order 4. ENTODINIOMORPHIDA Reichenow in Doflein and Reichenow, 1929

Another highly differentiated group of spirotrichs with much of its specialization possibly attributable to the mode of life, all species being found as endocommensals of herbivorous mammals. The great

reduction in somatic ciliature and the structure of the AZM suggest that the forms comprising this order have arisen perhaps directly from some oligotrichous stock.

Sharp's classical work (1914) on *Epidinium,* in which, incidentally, the neuromotor concept was introduced into protozoology, illustrated the anatomical complexity of these forms. The outstanding monographic work on the ophryoscolecids, which comprise the majority of entodiniomorphid species, has been done by the prolific Russian protozoologist Dogiel (e.g., Dogiel, 1927).

Morphogenesis, in particular stomatogenesis, has been little studied with techniques which reveal subpellicular structures, such as the silver impregnation methods. In a paper published well before the turn of the century Schuberg (1891) noted that the new "peristome" develops in a cavity beneath the body surface; in this respect stomatogenesis here appears to be very similar to that discussed above for certain of the oligotrichs.

Jacobson (1931) and Bretschneider (1934), employing Klein's dry silver method in study of several ophryoscolecids, did demonstrate subpellicularly located silverlines which appeared to join regularly arranged basal granules; but little more than mention of their possibly important discovery was made and conditions were not studied in dividing organisms. Confirmation of a true somatic infraciliature in the ENTODINIOMORPHIDA might prove to be of considerable phylogenetic value, and its possible involvement in the morphogenetics of fission and stomatogenesis merits careful investigation. In species of several genera an infraciliature is consistently being found, at the time of this writing, in material impregnated with silver by the Chatton-Lwoff technique (personal communication from Mr. Sidney Kantor).

The relationship of the so-called dorsal zone of membranelles of the ophryoscolecids to the AZM (see Pl. IV, Fig. 3) has been studied in detail, particularly by such workers as Sharp (1914) and Dogiel (1927). From the point of view of evolution it appears that the DZM has been derived from the AZM, originally probably merely by extension with subsequent independent development, elaboration, and, in some instances, restricted localization. Comparative investigation of the infraciliary counterparts of these membranellar complexes, involving a series of genera, might be very helpful in further elucidation of their past histories.

Only two families comprise this order; representative genera include *Entodinium, Epidinium* (Pl. IV, Fig. 3), *Ophryoscolex,* and *Cycloposthium.*

Order 5. CTENOSTOMATIDA[11] Kahl, 1932

Another curious group, comprising fewer than three dozen species. Laterally compressed, the ctenostomes show very sparse somatic ciliature and even the buccal ciliature, as represented by the AZM, is reduced in size and extent. The firm pellicle, termed a carapace, is differentiated into longitudinal plates.

These ciliates are assumed to be spirotrichs; they certainly do not appear to possess any holotrichous characteristics,

[11] Sawaya (1940), in the interests of alleviating possible confusion, proposes "Odontostomata" as a new name for the ctenostome ciliates because of the existence of the well-established bryozoan order Ctenostomata Busk, 1852. In the Copenhagen Decisions (Hemming, 1953, p. 42) it is stated that any problems of homonymy between names of taxa in the higher groups should be resolved by the International Commission on Zoological Nomenclature. Pending some action regarding the matter, the writer, at least throughout the present paper, shall retain the name CTENOSTOMATIDA, since it is commonly associated with these particular ciliates by protozoologists. [Since this paper went to press, however, I have reconsidered the problem in detail and have decided in favor of supporting ODONTOSTOMATIDA as the proper name to be used pending an Opinion from the Commission, in view of the serious confusion which may result from allowing continuation of the homonymy.]

although to which spirotrichous group they are most closely related remains unknown. Precise studies of their infraciliature, fission, and stomatogenesis have not been made; in fact, practically no attention has been paid these sapropelic (or polysaprobic) ciliates during the past twenty-five years. Kahl has carried out the most authoritative work on the group (see Kahl, 1930–1935).

Representative genera include *Epalxis* (Pl. IV, Fig. 4), *Saprodinium,* and *Discomorpha.*

Order 6. HYPOTRICHIDA Stein, 1859

One of the better known orders of the whole subphylum Ciliophora; dorsoventrally flattened forms, with rigid pellicle, generally believed to represent the pinnacle of evolution in structural differentiation among the ciliates. Simple somatic ciliature has disappeared entirely, having been replaced by the versatile organelle known as the cirrus, a compound ciliary structure [12] seen infrequently, if at all, in other orders. Cirri are generally confined to the ventral surface, present in patterns of taxonomic value within the order. Sometimes they have undergone truly hypertelic development. Although typically tapered to a point, some are characteristically frayed at the distal end. Dorsally are often to be found the so-called sensory or tactile bristles, also organelles of ciliary origin (see footnote 12). The peristomial field is typically extensive and the AZM prominently developed. A UM is commonly present, although often inconspicuous in contrast to the AZM. Occasionally a supernumerary membrane, of unknown origin, appears in the buccal cavity (as, for example, in the species of *Diophrys* portrayed in Pl. IV, Fig. 6).

Perhaps further evidence of the highly evolved condition of this order may be seen in the structure and reactions of the macronucleus, matters in great need of renewed study with such techniques as electron microscopy. Probably unique in the subphylum Ciliophora, for example, are the curious, complex reorganization bands seen in the macronucleus of prefission forms of various species of hypotrichs.

The most significant work on the morphogenetics of fission and stomatogenesis is that of Chatton and Séguéla (1940). With characteristic precision and with beautiful application of the French silver method, these investigators demonstrated that the genetic continuity of the somatic infraciliature, as represented by the bases of the highly evolved cirri, is carried out just as faithfully as in holotrichous ciliates. They also showed that the buccal apparatus of the posterior daughter, the *opisthe,* in fission, arises from a very small kinetosomal anlage which in turn has been derived, presumably, from the parental apparatus. Thus stomatogenesis appears to be of an autonomous type very similar to that described for the heterotrich *Licnophora,* for the oligotrichs, and as probably exists among other less studied spirotrichous groups. As has been mentioned in preceding pages, genera in various holotrichous orders also exhibit autonomization of the ciliary buccal system.

The fascinating morphogenetic movements involved in migration of the anlagen of the new ventral cirri were first studied with painstaking care over fifty years ago (Wallengren, 1900, 1901); again in detail by Chatton and Séguéla (1940); and most recently by Bonner (1954), who made a precise quantitative study of the conditions which obtain in one species of *Euplotes.*

Hypotrichs have long served as favorite experimental material for workers interested in regeneration and morphogenesis,

[12] Very recent work with the electron microscope (Roth, 1955) has demonstrated that the individual ciliary components of a cirrus are identical, in ultrastructure, with simple cilia, and, furthermore, that no enveloping sheath exists as a definitive part of the organelle. The dorsal "sensory(?) bristles" seem, morphologically, to be nothing more than very short, small cilia, rather than unique structures.

being closely rivalled only by such heterotrichous genera as *Stentor:* the reader is referred to the papers by Balamuth (1940), Fauré-Fremiet (1945*a*), and Weisz (1954) for discussion of their wide usage in such work.

Representative genera include *Euplotes, Oxytricha, Uroleptus,* and *Diophrys* (Pl. IV, Fig. 6).

The Ciliate Genealogical Tree

Only three protozoologists since Bütschli have been bold enough to publish a reasonably full phylogenetic tree for the ciliated protozoa, as far as I have been able to determine: the first was presented by the Russian Schewiakoff (1896), the second about a quarter of a century later, by the Rumanian Lepşi (1926), and the third, after another span of a quarter century, by Fauré-Fremiet (1950*a*). Thus it would appear that another completely original attempt is not due until 1975; so the scheme offered here is essentially that found in Table IV of the last cited work, expanded somewhat and slightly modified and refined according to the writer's own ideas on the subject.

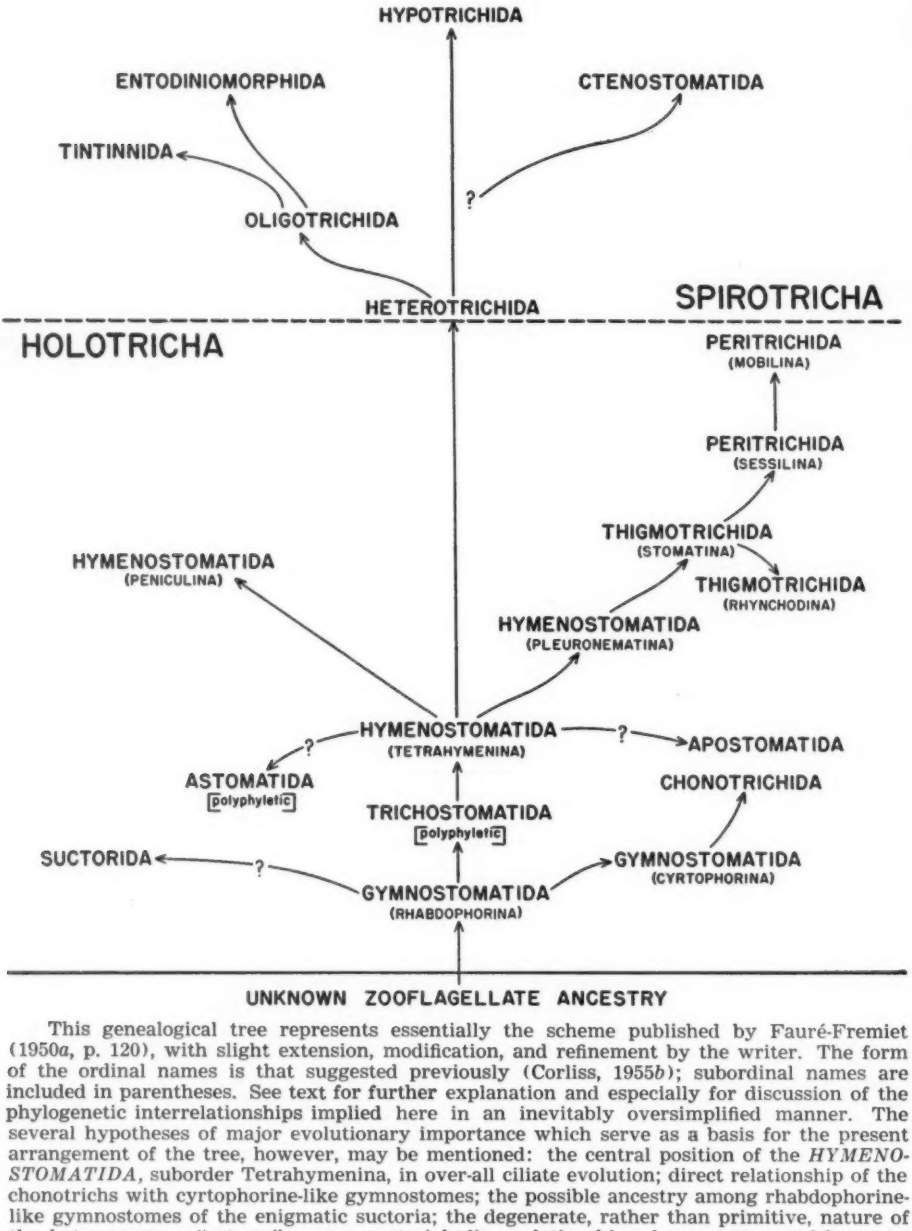
Since the arrangement on the trunk and along the branches, although perhaps highly speculative in places, is in complete accord with the discussions offered under the fifteen ordinal groups treated in the preceding pages, there is no need for extended discussion here. A brief recapitulation, however, along with the tree, may serve as a convenient summary of the subject under consideration, the new systematics of the ciliated protozoa. There would be no particular value in reviewing here either the long outmoded tree of Schewiakoff (1896, facing p. 114) or the briefly offered scheme of Lepşi (1926, p. 27).

The most primitive gymnostomes, in their structure, infraciliature, mechanics of fission and modes of stomatogenesis, appear to belong at the base of the tree; their own origin remains a mystery, although some sort of zooflagellate ancestry is always assumed.[13] This is not meant to imply, however, direct origin from present-day highly evolved flagellates such as the OPALINIDA and the HYPERMASTIGIDA. The chonotrichs, no longer representing such an enigmatic factor, may be placed on the end of a low branch just beyond the cyrtophorine gymnostomes. Possibly the suctoria arose from ancient rhabdophorine-like gymnostomes; that problem may remain insoluble. Surely these tentacle-bearing forms have enjoyed a long evolutionary history of their own.

Presumably back on the main evolutionary line, the genuine trichostomes are postulated to have arisen from gymnostome stock. As evidence of an increasing anatomical complexity, particularly in the area of the mouth, one finds consistently a true vestibulum here; but during the morphogenetics of fission the symmetry and form of a most primitive rhabdophorine gymnostome is realized once again. Some present-day "trichostomes" will have to be removed to render the group a more homogeneous one. The transition by way of the more complex trichostomes, which in their own ontogenies still neatly recapitulate the simple gymnostome pattern of fission, to the lower hymenostomes generally is considered a natural one. But much work remains to be done in this area. It is conceivable, in spite of the tacit assumption that a straight-line relationship (gymnostome → trichostome → hymenostome) exists, as illustrated in Table II, that various hymenostome and trichostome groups have sprung independently from diverse gymnostome stocks. Certain highly evolved gymnostomes do show evidences of some sort of vestibular ciliature; perhaps transition from such ciliature to true membranelles could have

[13] Minchin's conclusion (1912, p. 455) of some 45 years ago holds just as true today—after brief discussion of this problem of ciliate origin he summarizes the situation thus: "From these various considerations, it seems highly probable that the Ciliata are descended from flagellate ancestors; but it is not possible at present to indicate with any approach to exactness the line of descent."

TABLE II.—A PROPOSED PHYLOGENETIC TREE OF THE ORDERS AND SUBORDERS COMPRISING THE PROTOZOAN SUBPHYLUM CILIOPHORA



This genealogical tree represents essentially the scheme published by Fauré-Fremiet (1950*a*, p. 120), with slight extension, modification, and refinement by the writer. The form of the ordinal names is that suggested previously (Corliss, 1955*b*); subordinal names are included in parentheses. See text for further explanation and especially for discussion of the phylogenetic interrelationships implied here in an inevitably oversimplified manner. The several hypotheses of major evolutionary importance which serve as a basis for the present arrangement of the tree, however, may be mentioned: the central position of the *HYMENOSTOMATIDA*, suborder Tetrahymenina, in over-all ciliate evolution; direct relationship of the chonotrichs with cyrtophorine-like gymnostomes; the possible ancestry among rhabdophorine-like gymnostomes of the enigmatic suctoria; the degenerate, rather than primitive, nature of the heterogeneous "astome" group; a straight-line relationship of gymnostome-trichostome-hymenostome stocks; kinship of the specialized peritrichs with hymenostomes through the thigmotrichs; and the origin of the entire, compact spirotrichous assemblage from holotrichs of a tetrahymenal hymenostome type.

taken place without direct involvement of any kind of trichostome we know today.

Notwithstanding the above-mentioned uncertainties, the hymenostomes may be considered to be the first ciliates to show a genuine buccal or peristomial cavity, equipped with truly compound buccal ciliature organized fundamentally in a tetrahymenal pattern; a vestibulum may or may not be present. This first appearance of buccal organelles represents a major advance over the gymnostomes and trichostomes; at the same time, the primitive nature of the AZM as typically seen here reflects the potentialities of the order from the point of view of further evolution. The mode of fission is typically a straightforward homothetigenic one but variety exists in patterns of stomatogenesis; such diversity again may be interpreted as indicating a plasticity of great potential importance in phylogeny. The more primitive hymenostomes, the Tetrahymenina, may be considered to have been a center of divergence in three major directions: first, to the dead-end Peniculina group; second, to the Pleuronematina group; third, onward and upward to the entire spirotrichous assemblage of the Ciliophora.

The astomes and apostomes also may have evolved directly from primitive hymenostome-like ciliates, but information is scanty here. Perhaps the polyphyletic collection of forms currently included among the astomes will make it unwise to retain any of them in a distinct order of their own. The mouthless condition seems clearly to be a characteristic secondarily acquired, rather than serving as evidence of primitiveness. The symbiotic mode of life of both groups, astomes and apostomes, complicates attempts at recognizing true structural homologies with other holotrichous orders.

The branch through hymenostomes of the Pleuronematina group leads to the thigmotrichs and on to the highly specialized peritrichous assemblage. The hypothesis that this arrangement represents the true phylogenetic picture is one of the most significant contributions of Fauré-Fremiet to the new systematics of the ciliates. There is considerable evidence to support the theory, much of it based upon long-known data reinterpretable in the light of newer information. But without the silver impregnation technique, with its precise and consistent revelation of the infraciliature, and without the suggestion of the existence of truly homologous buccal organelles in the seemingly diverse groups (hymenostomes and peritrichs), the phylogenetic relationship believed to exist here could not have been formulated so convincingly. At the same time it should be stressed that many vexing questions remain unanswered and many pertinent problems unsolved; revisions anew undoubtedly will be necessary at all levels as our knowledge increases.

The stretch from the hymenostomes to the heterotrichs is a long one, yet it is generally agreed that spirotrichs have evolved from holotrichs and the two groups named seem most logically implicated by all data available. It is reassuring to have support from the morphogenetics of fission and stomatogenesis. Recognition of AZM-bearing main-line holotrichs is imperative: the heuristic Furgason-Fauré-Fremiet hypothesis contains this important postulation. No longer can holotrichs, as a group, be said to be totally without an adoral zone of buccal membranelles, even exclusive of the peritrichous forms now among them.

Within the smaller, more compact second subclass, the Spirotricha, problems of phylogenetic relationships do not seem so great. Specialization and diversity cloud the evolutionary picture but all groups would appear to have arisen directly (or just once-removed) from the large and relatively plastic order of heterotrichous forms.

The pinnacle of pellicular differentiation among the whole Ciliophora is exemplified by the hypotrichs. While most higher spirotrichs have simply lost their somatic ciliature, the hypotrichs have had

theirs molded into highly specialized compound structures (the cirri) with eventual restriction of these organelles to the undersurface of the rigid, dorsoventrally flattened body. At the same time the AZM, prominently displayed, is retained in full bloom. Complete reorganization (i.e., total dedifferentiation) of pellicular structures during the morphogenetics of fission and regeneration, with retention, nonetheless, of genetic continuity in the infraciliature, is accompanied in the hypotrichs by presumably full autonomization of the buccal apparatus in stomatogenesis.

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Points of View

Problems of Family Nomenclature

Recent discussion by Arkell (1954, 1955), Sabrosky (1954), and Follett (1956) of the modifications to the International Rules of Zoological Nomenclature proposed at Copenhagen with regard to the naming of families is accentuated by certain proposals now before the International Commission for consideration. These proposals, submitted by A. E. Ellis (1956), concern primarily the official listing of three well-known generic names for freshwater Mollusca, and, as an addendum, the three family names based on these genera are recommended for addition to the Official List.

The generic names involved are *Unio* Philipsson, *Lymnaea* Lamarck, and *Margaritifera* Schumacher. Conservation of the first name necessitates stabilisation of the other two names. The family names based on the first two genera, Unionidae Fleming and Lymnaeidae Rafinesque, have been in use for many years and their authorship and validity are not in question. However, the proposal to add to the Official List the name Family Margaritiferidae Haas, 1940, raises several questions.

For many years the generic name *Margaritana* Schumacher, 1817 was used for the taxon which includes the species *Mya margaritifera* Linné. The type species of *Margaritana* is, by monotypy, *Margaritana fluviatilis* Schumacher, a substitute name for *M. margaritifera* Linné. However, Kennard, Salisbury and Woodward (1925) brought to light an earlier generic name for this taxon, *Margaritifera* Schumacher, 1816 (a valid emendation of *Margartifera*). The type species is again, by monotypy, *fluviatilis* Schumacher and *Margaritana* is thus a junior objective synonym of *Margaritifera*. The latter name is now used almost exclusively for this group.

Ellis, on the authority of Dr. L. Cox, states that Haas (1940) was the first to use the family name Margaritiferidae and therefore proposes to have that name included in the Official List credited to Haas as author. While it is possibly true that Haas was the first to write "Margaritiferidae," he was not the first person to recognise the family status of this group of mollusks. Ortmann (1909) first separated the group from the family Unionidae as a subfamily and later (1911) elevated it to full family rank. However, since the generic name then accepted was *Margaritana* Schumacher, Ortmann wrote Margaritaninae and Margaritanidae. This usage persisted for many years, but the first person after 1925 (that is, after the discovery of the prior *Margaritifera*) to emend the family name in conformity with Article 5 of the old rules appears to have been Haas. He simply wrote "Family Margaritiferidae" at the head of a list of species and it is quite obvious from the context that Haas was not claiming to have done anything new; he was simply following the rules then in operation. Under the old rules, the question of the author of a family name was not considered. There was nothing to say that the author of the emended family name in this case should not still be regarded as Ortmann. In fact, another worker (Modell, 1942) has since written "Family Margaritiferidae Ortmann, 1911."

It should also be remembered that if the family name had not been emended prior to 1953, it would now have to remain unchanged as Margaritanidae Ortmann in accordance with C.D.Z.N., p. 36, par. 54, (1)(a).

The problems which arise in connection with this family name are as follows. Are the Copenhagen Decisions to be retroactive as Arkell (1954, 1955) claims, in which case we should have to return to

the older Margaritanidae, or are they not to be retroactive as Sabrosky (1954) claims and as the modifications proposed by Follett (1956) aim to ensure, in which case we shall continue to use the later Margaritiferidae? More important, who is the author of the name Margaritiferidae?

It would seem obviously desirable to continue the use of Margaritiferidae now that it has become more or less established, and it is hoped that Sabrosky's interpretation is correct or that Follett's proposals are accepted. I agree with Arkell that it would be highly undesirable to have forgotten family names based on invalid junior synonyms brought into use. At the same time, the preservation of well-known and established family names from frequent alteration based on subjective opinion is worthwhile.

There seems to be some inconsistency in outlook between C.D.Z.N., p. 36, par. 54, (1) (a) which allows a family name to be based on a generic name which is not necessarily the oldest available for the type genus, and par. 54, (1) (b) and the following Recommendation where it is implied that the family name *should* be based on the oldest available name.

Neither the old rules nor the new proposals state definitely who is to be considered the author of a name which was emended under the old Article 5, unless C.D.Z.N., p. 36, par. 53, (1) is to be construed as establishing authorship from the date of first usage. Although there is a parallel between this type of emendation and that of an author publishing a new name for an invalid junior homonym, there is a subtle difference. In the latter case, credit for the new name is given to its author even though he was not the first to recognise the group as a zoological entity, but he is at least required to think up a new name. In the case of an emendation to a family name under the old rules however, no originality is required of the emending author, other than a knowledge of the rules and knowledge of the invalidity of the generic name on which the family is based. In the present case, Haas' emendation required only a knowledge of Kennard, Salisbury and Woodward's paper and the application of an automatic adjustment. There is a closer parallel between this type of emendation and the Valid Emendation of a generic or specific name which has been incorrectly formed or based on a misspelling.

It seems wrong to take credit away from Ortmann for the family name, especially in view of the vital part which he played in solving the many problems of classification in this most complex group of animals. The ideal solution seems to be to use the name Margaritiferidae Ortmann, 1909, as a Valid Emendation of Margaritanidae Ortmann.

It seems clear that some definite statement should be included in the new rules as to the person who is to be regarded as the author of a family name emended under the old rules. The comments of other zoologists interested in this matter would be welcome.

The problems raised here are brought to the attention of zoologists as indicative of the complexity of modern nomenclatural rules and of the sort of questions which are bound to arise when further attempts are made to stabilise family names. The matter should receive urgent attention from those responsible for drafting the new rules in order that confusion should not prevail.

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The Taxonomic Significance of Gaps in Pelecypod Morphology

> The systematic study of Mollusca has resulted, like that of other groups, in the production of a classification based on the principles of "adult seriation." Groups and sub-groups are defined ostensibly by their possession of certain combinations of positive characters; but the real basis is the occurrence of gaps, some large and deep, others slight, in the series of adults available for examination. As knowledge increases, these gaps are often reduced or filled up, and the positive characters defining the groups are then altered accordingly. But some gaps in the seriation remain obdurate: the more we know the sharper they become.
>
> —WALTER GARSTANG, 1929, p. 83.

This is certainly as true today as it was in 1929, at least as far as the classification of the Pelecypoda is concerned. In the case of the pelecypods, the familial level is the lowest one at which major gaps occur, and these gaps are the basis for distinguishing between families. (In a few cases the superfamily or the subfamily is the compact morphologic unit; but for purposes of this discussion the term "family" is intended to embrace all of the familial categories.) The importance of the family level could change in the course of time, with increasing knowledge. For example, in the first third of the nineteenth century the generic level was the important one for grouping pelecypods, but since that time the trend toward finer splitting has necessitated generalization at a continually higher level.

Why is the family category so important in pelecypod classification? As a museum paleontologist, I find it the pragmatic category in my work, and I dare say that this is also true for many other paleontologists and neontologists who do taxonomic work on pelecypods. For example, I may receive for identification a large collection of Miocene pelecypods from the cliffs along Chesapeake Bay. I do not attempt to sort the material immediately by genera and species. Instead, I am most likely to pick up each fossil shell and say to myself, "a pectinid, a venerid, an astartid, a cardiid," and so on until the bulk of the material has been sorted. A few rare or unusual shells may at first escape familial allocation, but the great majority are sorted in this way. Only as a secondary step do I then consult faunal monographs to identify the genera and species.

(It should be pointed out that lack of knowledge precludes such a systematic approach to Triassic and older pelecypods.)

In these times of emphasis on species, subspecies, and lower categories in taxonomy, we are prone to forget some of our routine procedure as systematists. Furthermore, we are even more prone to overlook the significance of our routine work as it relates to the general classification of the groups in which we specialize.

In the higher categories the presence of morphologic gaps is of basic importance in our classification. Whether these gaps are real or apparent is not within the discussion of the present paper. We rely on these gaps in our day-to-day taxonomic research, and certainly without them our taxonomic tasks would be much more arduous if not impossible.

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Taxonomic Characters in Mollusca

Are we not describing or establishing a multitude of genera based on no more than specific characters?

A very good new book has been published this year on the Cypraeidae. The compilation and discussion of species will make it indispensable to the worker in this group. However, the author has followed the current trend in this field. The genus *Cypraea* Linné, 1758 is now composed of 13 subfamilies and 52 genera based on variations of the same general morphological characters. It has been facetiously said that we will soon have every species in a genus of its own, thus simplifying the nomenclature by entirely eliminating the necessity for such a taxon as species.

The basic purpose of all systematics must be the identification of the animals involved, and it would seem logical not to make the system unnecessarily complex. Construction of a taxonomic system to contain the species of one province involves no great problem when compared with that of a large world-wide collection, not to mention the host of variations in the fossil.

Occasionally a student will confine his work to the fauna of one locality, refusing to examine or consider specimens from any other province. While it is true that this is no doubt the day of the specialist, the fact remains that such a worker will necessarily be so much a victim of his bias that anything he may publish will probably be nonsense. To be meaningful, his systematic divisions must relate groups, not only throughout the earth in space, but vertically in time.

The following suggestions are offered for consideration before the entire systematic structure for conchology becomes too nebulous for any to comprehend.

1. *Genus* should be broad and based on characters of constant and wide occurrence. It is assumed that these will be easily accessible external morphological characters. When there may be an anatomical distinction, this should be accepted as the single exception to the rule.
2. *Subgenus* should be based on diagnostic characters of limited occurrence.
3. *Species* should be based on heritable characters not affected by environment.
4. *Subspecies* should be based on characters resulting from environment.
5. *Form* should include all variations within a species from one province.

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Erratum

In "A note on the relationship of the hemipteroid insects" by Lewis J. Stannord, Jr. (SYST. ZOOL., *5* (No. 2): 94-95), the citation to Ross should read:

Ross, H. H. 1955. The evolution of the insect orders. *Ent. News, 66:* 197-208.

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